MALACOLOGIA, 2014, 57(1): 1-97

DECONSTRUCTING DENDROPOMA: A SYSTEMATIC REVISION OF A WORLD-WIDE WORM-SNAIL GROUP, WITH DESCRIPTIONS OF NEW GENERA (CAENOGASTROPODA: VERMETIDAE)

Rosemary Е. Golding!.2, Rüdiger Bielert”, Timothy A. Rawlings? & Timothy M. Collins4

ABSTRACT

Identifying natural groups within the caenogastropod family Vermetidae has proven challeng-
ing. The sessile lifestyle of vermetids, with associated xenomorphically distorted, overgrown
and corroded shells, has resulted in a long and confused taxonomic history based primarily on adult shell characters. In this study, we use morphological, anatomical and molecular data to clarify systematics and phylogenetic relationships within the genus Dendropoma $.1. We assess generic names previously used in the Dendropoma group for availability and recognize Veristoa Iredale, 1937, as a junior synonym of Dendropoma Mörch, 1861. We describe 21 species, eight of which are new, place them into four robustly supported genera (Dendropoma s.s.; Novastoa Finlay, 1926; Ceraesignum п. gen.; Cupolaconcha п. gen.), and outline the current state of knowledge of the distribution of these taxa. The genus Dendropoma s.s. is well supported in our phylogenetic analysis and is additionally supported by features of the operculum, reproductive traits and a novel mitochondrial gene order. Among the four genera, members of Dendropoma s.s. alone maintain unstalked egg capsules in the mantle cavity rather than attaching them to the shell via a slit in the female mantle. The opercula of examined species within the genus Novastoa are characterized by a well-developed mammilla on the internal surface and upright tightly packed spiral lamina on the external surface. In Ceraesignum n. gen., the operculum lacks a mammilla and displays a fingerprint-like texture on its inner surface. The genera Ceraesignum n. gen. and Novastoa form a well-supported monophyletic group with the genus Dendropoma s.s., although sister group relationships among these genera are not resolved. The fourth genus, Cupolaconcha n. gen. is more closely related to the vermetid genera Eualetes Keen, 1971a, Thylaeodus Morch, 1860, and Petaloconchus Lea, 1843, demonstrating that Dendropoma s.l. is not a monophyletic group. The calcified operculum of Cupolaconcha n. gen. is unique in the Vermetidae and examined species in this genus are also characterized by a translocation of the valine mitochondrial tRNA. Further study will encompass the full range of morphological diversity in the Vermetidae
to clarify the major lineages within this remarkable family of snails.
Keywords: Taxonomy, evolution, reef-forming organisms, protoconch morphology, gene sequence order, molecular phylogeny.

INTRODUCTION

The caenogastropod family Vermetidae com-
prises at least 160 extant species of sessile,
suspension-feeding, irregularly coiled marine
snails found in warm temperate and tropi-cal oceans around the world. The taxonomy and nomenclatural history of this family of “worm-snails” is notoriously confused (Keen, 1961; Bieler & Petit, 2011), however, in part because their uncoiled and attached tubes

defy traditional classifications based on adult shell characters, in part because of a long and complex history that commingled nominal gastropod and polychaete taxa. Among the now recognized subgroups of Vermetidae is the genus Dendropoma Mörch, 1861, a name introduced by Mörch (1861: 153) as a Section of Siphonium (see below) and based on the
type species, by subsequent designation of
Keen (1961: 189), Siphonium (Dendropoma)
lituella Mörch, 1861.

1Invertebrates, Field Museum of Natural History, 1400 Lake Shore Drive, Chicago, Illinois 60605, U.S.A. 2Malacology, Australian Museum, 6 College Street, Sydney, NSW 2010, Australia
3Department of Biology, Cape Breton University, 1250 Grand Lake Road, Sydney, Nova Scotia, B1P 6L2, Canada 4Department of Biological Sciences, Florida International University, 11200 SW 8th St., Miami, Florida 33199, U.S.A. *Corresponding author: rbieler@fieldmuseum.org

The Dendropoma group is thought to include a wide range of vermetid species and morphol-ogies, ranging from the large and conspicuous coral reef dweller Dendropoma maximum (G. В. Sowerby I, 1825) of the Indo-Pacific (with a concave, corneous saucer-shaped opercu-lum), to gregarious Dendropoma corrodens (d’Orbigny, 1841) ofthe Caribbean (with a coni-cal operculum constructed of a spiral corneous lamella), to Dendropoma meroclistum Hadfield & Kay, 1972, from the Hawaiian Islands (with a bi-layered, partly calcified operculum). Focusing on aspects of protoconch morphol-ogy, Bandel & Kowalke (1997: 260 ff.) sepa-rated Dendropoma s.l. (specifically including D. maximum and D. meroclistum) from the remaining Vermetidae in a new subfamily “Den-dropominae” (emended to Dendropomatinae by Bieler & Petit, 2011: 11). The new nominal subfamily was described as including “vermetid gastropods with irregular teleoconch and regu-lar protoconch with a cancellate sculpture”). There are probably at least a few dozen living species belonging to Dendropoma s.!., but their number cannot yet be estimated with any confidence for three reasons: (1) Historic under-sampling: these sessile and often cryptic organisms are rarely collected during gen-eral collecting efforts and often excluded from regional biodiversity studies. (2) Taxonomic uncertainty: original species descriptions (and type specimens that often consist of tube fragments from vaguely indicated localities) cannot always be clearly recognized and linked to living populations. Their sessile mode of life allows rafting on natural and man-made structures and thus potential dispersal across oceans, confounding regional revisionary stud-ies. Also, the past near-random allocation of generic names, including both gastropods and polychaetes (e.g., genus Serpula Linnaeus, 1758, type of polychaete family Serpulidae) makes it extremely difficult to recognize subsets among the some 1,300 species-group names that have been in use for worm-snails (Bieler & Petit, 2011). (3) Hidden diversity in species complexes; recent molecular work by Calvo et al. (2009) has shown that the “well-recognized” reef building species Dendropoma petraeum (Monterosato, 1884) represents a species complex. Likewise, Faucci (2007) appears to have identified numerous cryptic species within her phylogeographic survey of six vermetid species across the Pacific.
The lack of a reliable taxonomic infrastructure for the Vermetidae has proved particularly challenging for marine ecologists given that ver-

GOLDING ETAL.

metids are a significant element of many marine warm temperate and tropical ecosystems. Within these environments, vermetids are well recognized for their role in habitat creation and modification, as well as interactions with other sessile animals. For instance, various species of Dendropoma are gregarious and form struc-turally complex platforms (“trottoirs”) and reefs in the subtropical and tropical waters of the Mediterranean, Bermuda, Brazil, Cape Verde Islands and Mexico (e.g., Antonioli et al., 1999). While otherwise poorly studied, these biogenic structures are known to greatly enhance region-al fish diversity and support a rich community of endolithic organisms, including crustaceans, polychaetes, sponges, sipunculids and bivalves (Thomas & Stevens, 1991; Goren & Galil, 2001). Reef-building vermetids have thus been considered critical “ecosystem engineers” in the marine environment (Coleman & Williams, 2002) — organisms that through morphologi-cal complexity have profound effects on local biodiversity. Changes in the abundance and distribution of reef-building vermetids can also have broader effects by influencing water flow, sedimentation and larval settlement patterns. Such responses have been noted with the loss of the rim of Dendropoma reefs along the rocky Mediterranean shores of Israel and the associated proliferation of invasive Red Sea mussels Brachidontes pharaonis (P. Fischer, 1870) (Rilov et al., 2004).
Vermetids, including Dendropoma s.l., are also well represented in sensitive and threat-ened marine habitats, including coral reefs (e.g., Peyrot-Clausade et al., 1992; Gischler & Ginsburg, 1996). Although their interactions with other coral reef organisms are poorly un-derstood, Dendropoma maximum and a guild of other vermetids including D. platypus, D. mero-clistum and D. gregarium, appear to negatively affect the growth, morphology and survival of reef building corals (Zvuloni et al., 2008; Shima etal., 2010, 2013). Such responses may be the direct or indirect effects of mucus “feeding nets” deployed by reef-dwelling vermetids (Zvuloni et al., 2008). Although such deleterious effects on corals can be ameliorated locally when protective guard crabs are present (Stier et al., 2010), reefs in the Red Sea and South Pacific are currently experiencing marked increases in vermetid density, a possible byproduct of human activities in coastal waters (e.g., eu-trophication, species introductions, coastal development) (Zvuloni et al., 2008; Shima et al., 2013). This dramatic change in baseline community structure underscores the need

“DENDROPOMA GROUP” WORM-SNAILS 3

to understand more fully the complex set of interrelationships among vermetids, corals, and other reef-dwelling organisms. Knowledge of vermetid systematics and ecol-ogy is also becoming increasingly important to the field of paleoclimatology. Vermetids are extremely reliable tools for interpreting past sea-level, sea temperature and productivity (e.g., Schiaparelli et al. 2006; Vescogni et al., 2008; Sisma-Ventura et al., 2009), and con-sequently, of great importance for predicting future climatic trends. For instance, Dendro-poma spp. and Petaloconchus varians, with their low intertidal distribution and purported narrow bathymetric ranges, have provided sea level estimates for the Brazilian coast span-ning the entire Holocene period (e.g., Laborel et al., 2000), with a hypothesized precision of 0.40-1.00 m (e.g., Angulo et al., 1999, 2002). Similar paleoclimatological studies have been conducted in the Mediterranean based on D. petraeum (e.g., Morhange & Pirazzoli, 2005). Because of their often ubiquitous occurrence in temperate zones (in contrast to stony cor-als) and the possibility of performing 14С age determinations, vermetids are now formally used as Sea Surface Temperature (SST) prox-ies (Silenzi et al., 2004). Confusion regarding species’ identities and their true bathymetric ranges, however, is leading to concern over the widespread and uncritical use of vermetids as reliable paleoclimatic indicators, reinforc-ing the need for further systematic work (e.g., Schiaparelli et al., 2006).
To date, a molecular approach has not been formally employed as part of a systematic revision of the Vermetidae or its component groupings. Molecular tools and techniques have been applied to vermetids over the past decade, however, in an effort to interpret spe-cies boundaries (Calvo et al., 2009; Weinberger et al., 2010), explore phylogeographic structure (Faucci, 2007), as well as to place the Ver-metidae within the context of caenogastropod evolution (e.g., Colgan et al., 2007; Criscione & Ponder, 2012). Such studies have convinc-ingly demonstrated the utility of fast evolving mitochondrial DNA (mtDNA) genes (COI, rrnS, rmL) and nuclear genes (H3, 28S rRNA, ITS) in helping to discriminate among populations and species of vermetids (Faucci, 2007; Calvo et al., 2009), to identify cryptic species (Faucci, 2007; Calvo et al., 2009), to highlight cases of likely species introductions (Faucci, 2007; Weinberger et al., 2010), as well as to infer the role of physical processes on the pattern of speciation and divergence of vermetid taxa

(Faucci, 2007). Evidence of multiple mitochon-drial gene order rearrangements within the Vermetidae has also suggested the possibility of using derived mtDNA gene order patterns to define monophyletic lineages of vermetids (Rawlings et al., 2001, 2010). A molecular ap-proach thus holds great potential for helping to build a stable taxonomic framework for this family.
This study aims to examine the systematic diversity and evolutionary relationships of the group of worm-snails currently assigned to Dendropoma. The taxa included herein were chosen to represent the breadth of morphologi-cal diversity in this group, but this study does not yet provide a comprehensive systematic revision of all species in this complex. The primary aim of this study is to generate morpho-logical/anatomical data suitable for a genus-level revision of the group, sampling across the newly recognized morphological diversity. In order to re-evaluate the composition of genera, previously introduced genus-group taxa will be assessed. In addition to the development of a set of morphological characters to distinguish each group, we will use a molecular phylogeny to examine the monophyly of Dendropoma and other newly morphologically defined groups. We intend to develop a molecular framework and a set of morphological characters to distinguish each group and to allow for the accurate systematic placement of established and previously undescribed species of Den-dropoma s.!.

MATERIALS AND METHODS

Material

The specimens examined during this study were sourced primarily from the collections of the Field Museum of Natural History (FMNH; based on numerous vermetid-focused expedi-tions, see below) and the Australian Museum (AM). Additional material was loaned by the Florida Museum of Natural History at the Uni-versity of Florida (UF), the California Academy of Sciences (CASIZ) and the Museum of New Zealand Te Papa Tongarewa (NMNZ). Further specimens for this study were donated to the Field Museum collections by M. Calvo and J. Templado (material from the Mediterranean); L. Gosselin (material from western Canada); M. G. Hadfield, A. Faucci, R. Strathmann and M. Strathmann (material from the Hawaiian Islands); I. Kappner (material from Jordan and

4 GOLDING ET AL.

Cape Verdes); P. M. Mikkelsen (material from
Bahamas, Barbados and Florida); J. Norenberg
(material from California); A. Pacheco (mate-
rial from mainland Chile); N. Phillips and S. Schiaparelli (material from French Polynesia);
U. Safriel (material from Sinai); J. D. Taylor (material from the Maldives and Kenya); and J. Worsfold (Bahamas). The Material Exam-ined sections of the systematic descriptions presented here include specimen counts in some cases. However, where the examined lot comprises a chunk of “vermetid crust” (referred to here as an aggregate matrix) removed from the surface of the substratum, it was usually not possible to provide a precise specimen count and the count is estimated as “many”.

Field Work

The material and observations on which this study is based come from vermetid-focused field work in many locales, including: Bahamas (Grand Bahama, New Providence; April 1993, August 1994 [RB]; Andros, March 2004 [TR]; Abaco August 2012 [RB, TC]); Barbados (Au-gust 2010 [RG, TR]); Belize (Carrie Bow Cay; 1986 [RB], 2011 [RB, RG, TC, TR]); Bermuda (Bermuda Biological Station/Aquarium; March 1983, May 1988 [RB]); British Virgin Islands (Guana; August 2010 [RB, TC]); Cayman Is-lands (Grand Cayman; January 2011 [Lauren Dombowsky for this project]); Chilean offshore Islands (Juan Fernandez Archipelago and Desventuradas Islands; 1997 [RB]); Dominica, August 1978 [RB]; East Florida and the Florida Keys (Smithsonian Marine Station, Ft. Pierce; Summerland Mote Lab, etc.; 1985-2012 [RB]; Peanut Island; 1997 [TR]); Hawaiian Islands (Oahu; Kewalo Marine Laboratory, etc.; De-cember 1986, March 1988, June 1995 [RB]); Netherlands Antilles (Saba; August 1996, October 2010 [RB]; St. Martin, August 1996 [RB]); St. Lucia, August 1978 [RB]; U.S. Virgin Islands (West Indies Laboratory, St. Croix; February 1987 [RB]); Venezuela (INTECMAR station, Puerto Cabello, etc.; 1986 [RB]); West-ern Australia (Houtman Abrolhos Archipelago; Мау 1994 [RB]).
Worm-snails were collected during field work using a variety of specialized techniques tailored to maximize the success of locating and obtaining intact specimens. Intertidal or shallow subtidal vermetid habitat was accessed by snorkeling (Fig. 1) and deeper sites were surveyed using SCUBA (Fig. 2). In both cases, specimens were located by eye, and a ham-mer and chisel (or screwdriver) were used to

remove either the specimen alone, a chunk of substratum with the vermetid attached, or a section of “vermetid crust” in the case of reef-forming species. Care was taken to retrieve the specimen with an intact shell whenever pos-sible. Dead worm-snail shells were obtained by collecting objects on the shoreline that had been utilized as substratum by vermetids (Fig. 3), such as larger gastropod shells or echi-noderm tests. Key vermetid habitats include stones, coral rubble, living coral heads (Fig. 4) and gorgonian stems and holdfasts (Fig. 5).

Anatomical and Morphological Studies

Where possible, animals were collected alive and photographed to record coloration of the head-foot and mantle. In most cases, this was not possible, and only preserved material was available. The systematic anatomical descrip-tions below are based on both dry and wet (ethanol and formalin preserved) specimens. If only dry material was available, individual dried bodies were removed from their shells and rehydrated in distilled water to allow partial description of the soft tissue anatomy. Individual shells and clusters of shells at-tached to the substratum were photographed using a digital camera (attached to a stereo microscope if very small) or alive in the field us-ing a digital camera in an underwater housing. Shell measurements were made using digital calipers to record the following parameters:
(1) maximum aperture diameter; (2) length of shell (i.e. greatest length in any direction); (3) diameter of last whorl (sometimes equal to length of shell, if concentrically coiled). The coil-ing pattern was categorized as: (1) concentric;
(2) initially concentric but becoming off-center;
(3) “Turritella-squeezed-sideways”, a recogniz-able pattern unique to some vermetids [a term first applied to a species of Petaloconchus by Carpenter (1857: 309)]; or (4) irregular. Proto-conchs were sometimes obtained directly from adult shells, but overgrowth by the postlarval shell often hindered obtaining a clean speci-men. In most cases, recently settled juveniles were removed from the substratum around adult worm-snails and — often after com-parison with hatchlings or adult protoconchs — presumed to belong to the same species. Intracapsular larval shells were also examined when found, and although they may not have reached settlement size they were clean and ideal for observing sculpture. Opercula were photographed using a digital camera attached to a microscope to record color.

“DENDROPOMA GROUP” WORM-SNAILS 3

Shells, protoconchs and opercula were cleaned of encrusting algae by immersion in an ultrasonic water bath and examined using SEM to observe sculpture and protoconch shape. Buccal masses were extracted manually from dissected specimens and radulae cleaned by soaking in 10% NaOH solution for about four hours at 60°C, then rinsed in distilled water and ethanol. At least two radulae were examined by SEM from each species and the maximum number of rows and length о the ribbon were re-corded. Specimens to be imaged by SEM were mounted on conductive carbon tabs, coated in gold and examined using a Leo EVO 60 SEM.

The anatomical descriptions based on dis-sected specimens include aspects of the external morphology (including coloration in life, if possible, and in preserved specimens), pallial anatomy (including the pallial reproduc-tive system), and egg capsules recovered from brooding females. Specimens were dissected under a stereomicroscope and illustrated us-ing a drawing tube attachment. Anatomy was
studied in two to ten specimens, except where
only one specimen was available. Comparative descriptions of each genus and
species in the Systematic Part are limited to
characters that are informative for distinguish-

FIGS. 1-5. Photographs of collecting methods employed and habitat utilized by Caribbean species of Dendropoma, Novastoa and Cupolaconcha at Carrie Bow Cay, Belize (April 2011). FIG. 1: Shallow subtidal reef where D. corrodens, С. диапа п. sp. and N. pholetor n. sp. occur on the exposed surfaces of living and dead coral heads; FIG. 2: Collecting D. nebulosum by SCUBA, using a hammer and screwdriver to remove specimens intact from the substratum in crevices between living coral tissue; FIG. 3: Empty shell of Pinna sp. collected from beach drift with shells of C. guana attached (arrows); FIG. 4: Dead coral head encrusted with coralline algae and dense aggregation of D. corrodens; FIG. 5: D. nebulosum (arrows) and D. corrodens co-occurring on the stems of a gorgonian covered with milleporid “fire coral”.

6 GOLDING ET AL.

ing taxa atthe equivalent level. Characters that
are variable within a population or consistent
within a genus are not included in species-level descriptions.

Molecular Systematics

Specimens preserved in 70-95% ethanol or RNAlater were used for DNA extraction. A complete list oftaxa sampled, including locality details and collector information, is provided in Table 1. Whenever possible, tissue was sampled from the same lots as those examined for morphological and anatomical characters. Additional representatives of other vermetid genera (Eualetes, Petaloconchus, Thylacodes, Thylaeodus, Vermetus) were also included in our analysis to determine their relationship to focal Dendropoma s./. taxa.
For most animals, DNA was extracted from pieces of the head/foot region; however, in cases of particularly small vermetids (e.g., Dendropoma corrodens and Cupolaconcha meroclista), the whole body was occasionally used. Two different methods of DNA extrac-tion were routinely employed: (1) the standard CTAB and phenol chloroform extraction proto-col described in Collins (1996) for molluscan tissue, and (2) QIAGEN’s silica gel membrane DNA-binding protocol as implemented in its DNeasy Tissue Kit (catalogue #: 69504) for animal tissues.
For DNA amplification and sequencing, we targeted both mitochondrial (mtDNA) and nuclear gene regions. For mtDNA, we amplified а > 1.5 kb fragment spanning domains III-IV of the small-subunit rRNA (775), an interven-ing tRNA valine (trnV), and domains I-IV of the large-subunit rRNA (rrnL) (Rawlings et al., 2001). Substantial interspecific variation ex-ists at the nucleotide level within this region of the genome, including changes in gene order within and among vermetid genera (Rawlings et al. 2001, 2010). In addition, we targeted a ~1,100 bp portion of the nuclear 28S rRNA gene. While much less variable than mtDNA, we have documented up to 2.5% difference (uncorr.-P distances) in nucleotide sequence of this gene region within the Vermetidae based on sampling so far (Rawlings et al., unpublished data).
We amplified the mtDNA region in 2-3 over-lapping chunks, since attempts at amplifying this region in one piece were rarely successful with standard PCR amplification kits. Given the gene order changes that have occurred

within this region, the size of the total product amplified was highly variable across taxa, ranging from 1621-2505 bp in length. For two-piece amplifications, we typicallyemployed the following primer pairs, based on universal primers listed in Palumbi (1996): Fragment A — 12SA (5’-АААСТСССАТТАСАТАССССА-CTAT-3’) or 12Sai (5’-АААСТАССАТТАСА-TACCCTATTAT-3’) in association with 16SA (S’-ATGTTTTTGATAAACAGGCG-3’); and Fragment В — 12SF (reverse complement of Palumbi’s 12Sb’ primer; 5 -GCACACATCGC-CCGTCGCTCT-3’) in combination with 16SBr (5`-ССОСТСТСААСТСАСАТСАССТ-3’). In some instances, however, these primer com-binations were not successful; consequently additional primers were designed and different primer combinations attempted. A full listing of the primer combinations used and the sizes of the resulting amplification products can be obtained from the authors.
The region of the 28S rRNA gene was amplified using primer pairs 28SD1F (5’-GG-GACTACCCCCTGAATTTAAGCAT-3’) and 28SD6R (5 -CCAGCTATCCTGAGGGAAACT-TCG-3’) designed by Park & О Foighil, 2000. Amplifications of this gene region were relatively straightforward, although some taxa exhibited length heteroplasmy resulting in stutters/over-lapping chromatograms beyond a specific point in the sequence. In such instances, we typically cloned the PCR amplification and sequenced the resulting clonal products with good results; alternatively, to avoid cloning, we designed internal sequencing primers to bind on the downstream side of the variable region on both forward and reverse strands.
Amplification of PCR products occurred in molecular labs spanning two different institu-tions (Florida International University, Cape Breton University) and utilizing different thermal cyclers and PCR chemistries. The general protocols for successful amplification of targeted gene regions, however, were as fol-lows. For each amplification, 1 ul of 1x or 1/10x dilutions of each genomic DNA extraction was used as the template in a 25-50 ul reaction volume that consisted of 1.5-2.0 mM MgCl, 1х PCR buffer, 0.5 uM of each primer, 200 uM of each dNTP, and 0.5-1.5 units of Taq DNA polymerase (depending on reaction volume). PCRs were performed in MJ peltier thermal cyclers (MJ Research PTC-200, MJ Mini) or a Stratagene Robocycler Gradient 96 thermal cycler. PCR conditions followed the general procedures outlined in Mikkelsen et al. (2006).

N

“DENDROPOMA

G

R

O

U

P

”

W

O

R

M

-

S

N

A

I

L

S

(сэпициоэ)

[usas uauidads 29u819/91 оч — Ума pajeydioaJa] 2161 Aey 9 рецрен
66££8SDM 6EFESSOM 7005 “JW Ms162 251 'N.9ErL a ‘пчео ‘Aeg ayosuey :lIeMeH “ys = unysuosossÁyl ewodompusg
2161 By 9 рецрен
86EE8SOM ZS7PZLWH HIN немен “W'S'N ZZZBLE HNWA wnuebalb ewodoipueq
M.vZS'79 'No¿1l ' 81 ‘PUEISI eueng
16858597 SZVESSOM OLOC ‘OL ‘au ‘Reg эичм 'SJ881 yojed ‘ш €—Z :spueisj UIBJIA чзвыа 6699ZE HNWA
M.c2S'+ 9 ‘N-99ÿ'8L 'Pueisj ечепэ
I6EESSOM LZZVE8SOM OLOZ‘OL gy ‘Лея энчм Julog Аэхчои| Jesu ‘ш 9-6 :SPUEJS] иблл чзвия ZL29ZE HNWS
0.02 М.579`68 ‘N.897E L
G6EE8GOM YEVESSOM “NO Y Où se09 }5эм ‘eg Sue XIS ‘Jee BUIBUU :sopeqieg 960/ZE HNWA
0.02 M.969'6S 'N.EZE'EL ‘ISE09]sey VELESSOM SEVESSOM “NO AL Où ‘Reg Jan1y ‘зщ JO эзеа pue SY201 эцо}зэщи :зоредаея G60/ZE HNNA
LLOZ “Sd M.£8088 'N.208'91
S6EE8GOM FEVESSOM ‘OL Y ‘OY ‘Ey ‘Keg моя aed “youne] jeoq шо MS ‘ше :3Z1199 Zy1/Z€ HNWA
(zr8L ‘AUBIqIO.P)
ZEEESSOM PPLSCCAV 1661 “NINA ‘GY M.6EZL8 ‘N.G/97 2 ‘Shey eplio]4 ‘Aey HNOSSIN :ерно- “W'S'N LZLE6Z HN SU9pO1I09 ешоаолриэа
(y881 ‘oYesoJs}uoN)
16558695 8718$$3\ 6661 Г 3.669°0 'N.£€9'Z€ 'soled эр oged :еюлпи| ‘шед$ 15еле$ HNWS шпэедеа ешодолриеа
[usas иэшюэ4$ ээиэлээл OU — VNA parel1di9814] (1981 ‘YdJOW)
O6EE8GOM EZFESTOM 7005 “JW Ms162 291 'N.9Er La ‘Aeg ayosuey 'nyeo иемен “Y'SN = sndfjejd ewodospueq
M.ZE0LL 'NoLy9'9Z ‘PUEISI ODeqy 32819 JO ЗМ SJ981 |
6G8EE8GOM ZZVESSOM 2102 ‘Sd ‘au ‘OY S,JSMIEM YO Joos Jae эр!з]по ‘ш 1-01 :seweyeg 0/0S€€ HNWNH
MoS1L0'18 'N.699y z ‘Shey ерио|- ‘АзипоЭ эолиои| (2181 ‘UAMIIIQ)
8855869) LrLSccdV 1661 :94 ‘еоел Aoy ‘иоцелеи! yo jos! чэзеа ‘ш 7 :ермо!- “WSN BESSLE HN winsojnqeu ewodospueq
ho adAquAs |ембио WON] М.619`0/ 'S.0LFE Z 8002 ‘uelpne7 9 оээцэва
L8EE8GOM LEVESSOM 9002 ‘dV ‘нем seuoweuy ‘w /| ‘зэцчоцИеи| einsuluad :a11yO ELLZLE HNWA esueuo]jfeu ewodo/pueg
1981 ‘UJION ewodoupusq

VNdIS8Z VNQHU 128\/1098[[09 Áyeso7] 4 Day seloeds
°99\ Yuegussg

`иэлб эле eJep ис!$$а99е Yueg
-U99 pue 10792/109 ‘Ашеэс| ‘(э1аепеле элэцм) SUBLUIDSdS JOYONOA 40} злэдшпи чоцед®бел wunssnyy Ausßojäyd ле|поэюш eu} ul pasn |емэеи| | FIGVL

GOLDING

E

T

AL.

(

s

e

n

u

n

u

o

s

)

MovZS'v9 Мо ¿pb "81 PUEIS|
ZLVESSOM 08EESSOM 0LOZ:D1 ‘EY eueno ‘Aeg oyu ‘SJ091 yojed ‘w z :spueis] иблл чзцыя 0049Z€ HNWA
Ms29E0L Z :N°.9£92
LLVE8SOM BLEE8GOM LOC ‘Sd ‘GY ‘puejsj 092qY J2819 JO IN SJ281 ‘WU 8-9 :seweyeg 9/09£8€ HNN
LL“SOdZ
OLFESSOM SLEEBSSOM ‘OL ‘ML ‘Où “ge M:002°88 ‘N.LGL'91 Ae) 329 9/97 ‘WU 2-1 :2Z1189 pSL/ZE HNWA ‘ds u виепб ey9uosejodno
M.€ve PL ‘S.v09L'Z
= LLEESGOM 2002 :SS ‘puejsj 11, edey ‘'ndejewej julog :eiseuÁjog UOU814 GLOZOS HNWS ‘ds eyouooejodng
6OVE8GOM 9LEEBSIA 002 ‘MM 3.82 Frl 'N.zreL'spueisj eueuen ‘eg обед :шепэ — 009158 AN 'qwos ‘и (2/61 Key ® рецрен)
SOVESSIM GLEEBSOM 8661 ‘HN Mo164'2S! 'N:9Er Le nyeo eg ayosuey :llemeH ‘Y'S'N 9098$ HN e]s!j90Jauw ey9uosejodno
`иэб ‘и ey9uogejodn:)

Mo£78'82 ‘SLT EE ‘ds U
10758469) ErLBEEFV ¿661 ‘Gy “oBejediyoly zapueulay чепг ‘э0$п/9 UOSUIGOY EIS] :э!49 9069$ НМИ!- —ю о$плоиозидол шпибэе)
М‘LEоS сC` 681
9OVESSIM VIEESSOM LOOZ ‘NO “pue¡s¡ ебиозолеч 'ndeynyoyy ‘и 2-0 :spuels] 4009 = 6 VEL 6Z AN
'‘(‘Á“9и|ygq) zui gooa1m os
GOVESSOM ESZHLLUNH 6661 MI [Ajuo ajdwes эп$$1] eqeby jo ¡ng :ueplor 12Z281€ HNINA шпиихеш шпиб!$эелэ)
"‘uиun subb iseela:)

M.€ve vl ‘S.vO9LZ 6ÿc/z-000c-WI
VOVESSIM ELEESSOM 2002 :SS “pue¡s| 1 edey 'ndejewej julod :elsauAjod youel4 dNHNW ‘ds eoJsenoN
LL“SOdZ
SOVESSOM ZLEEBSDA “DL Y ‘Où ‘ay M.2Z80'88 ‘N.£089 1 ‘89 Mog alle) jo q uoobe| :3ZIJ98 721 27€ HNWNA ‘ds ‘u4o0jajoyd LOJSPAON
M.€6ZZZ 'NoS€Zpz ‘PUEIS| soJpuy 8819 US914
ZOVESGOM LLEEBSOM 7005 ‘ML ‘зе маи JO JUIOd YO 210US810] ‘Jepieju! :seweyeg 05/25 HNWA ds ‘U $15иешецед EOJSEAON
LOVE8SOM OLEE8SGOM $002 ‘Gy MI Mo€S'ZZ NSP9 L “es ‘эшпл eiped :SepleA ade) 8/6L0€£ НМИ- ‘ds u SISUSPI8AOGEI POJSEAON
9Z6L ‘Aejul4 EOJsenoN

[uses uewuiseds a9usajal OU — VNA pajeydioa.d] 2/6, Alq 9 ренрен
0OFESSOM OEVE8SSOM 7005 “JW Mo164'2S! 'No9€bv LZ ‘пчео ‘leg ayosuey :llemeH "V'S'N = wnjeydesolesd ewodoipusq

VNdIS8Z VNdIW J82\/10798/[09 A12907 seweds
++ "99 Yuequss)

Boy

(penunuos)

Aloy

JOYCE = MM
‘збинмеч

Ayjowip=y 1 ‘SUi]09
AyyowıL=9L
‘yjeredeiyos

oueJa]s = $$
‘ииешцедс

рлецо! = Sy
:'бирюэ

Алешэзоч = OY

“Jajelg

fe)

Jebipny
=9Y

:plemusis

21184 = Sd
“USSISANIN

‘и

eined = WWd
:uuewyjens

Lune = SW
:рецрен

JEeYdI = HN
“Ulessos)

sino7 = 97
:SUI09

эыпел = 97
‘uswyeg
‘M = Gy

‘ореаше|

osof = IF
¿Bisqualon
uor = МГ
¿Jeuddey

е|эаез| = M]
:узнелэи|

UIOD = IND
“Skay

1э490}$и4ц9 = WO
‘099924

орм = dV
:!loone4

eyyosnuy = 4V

:2JS09

Buy = OV

:SUOIJEIASIA

M‘L(Ys8N. n6.See/8E1E9uu S' 0ryZ)

89609431

YBEESSOM

1661
:91

‘ypnowijeZ

‘yoeeg

SAG
пб
:spesnyoesse

‘Y'S'N

ZOG9EE

HNWA

взео!ило;

ejnpIdalg

M.8€0'09

‘N.ZbZ

97
'pueisj
Uoye1g

adey

(86/1
‘sneeuury)

219884

1V
GBEESSOM

2102
“ML

“y9esg

UOIUIWOG

'[ePINEJUI

:ецоэ$

BAON
‘epeued

90G9ES

HN

валози

CULO]

sdnoibino

“AB¡URpO/I[‘nA1J666 s Ie8uuG/al9 1sag]

(09)

=
OZCYE8GOMH

78888895

6661
:Э\

эпб!/|
08S
‘59107\

9058$

НМИЗ

зпдепьи}

"Jo
зпеииел

Е

zes,
‘IPIeuI8g

euonig

N
GLrESSOM

EIEESTOM

6661
Г

3.669'0

‘N.££9'ZS

'soled
эр
Oged
‘elon

‘UIEdS
66/25

нми+

зпдепьи}

зпэииед

=

0081
‘ulpneq

SNJBUUSBA

= О

2002

Ms1L98°191

‘NoL62
LZ

5
8Lb£859M

9GZY/INH

“SW
'SU'HN

‘0121087

suey

оемэу

'sejge}
Joyemees

:IEMEH

“W'S'N

72Z8LE

HNINA

‘ds
snpose¡4y

=

0981
‘YOO

snposejAyL

=

M.GGEL'GCL'N.E9E8

Er
alu]
рецшея

aus)

зэоцею$

EULEN

6161
‘lea

<
¿Ive8s9M

ZBEESSIM

1661
:97
рецшея

eu]
jo
juoY
ul
“¡epruaju!

mo]
:EIQUNIO9

чзцыя
‘epeued

P0GSZE

HNINF

S/SU8A8Jequou

snyouoso/ejey

à

.810°08

‘N.9S6'9Z

(6581
‘^ибю20.р)

A
91758695)

185886).

7661
“NINA
‘яч

MUNOZ

yoesg
Wied
‘punos

эаон
‘пемеэз

:ерно|-

"W'S'N

972/28

HNWA

SUBUEA

SNY9U090JEJO4

=.

eyg|
‘297
SNU9U090/2194

5M:(neNu. r.eZg6yE)LoV 22)O '°098Z

=
GLVESSOM

PSZPZLWH

1661
‘HL

‘AyunoD

yoesg
wed
‘PUEISI
зпиеэа

:ерыо|-

“W'S'N

EZZBLE

HNWA

вап]
sejsjenZ

ы

EL/6L
‘u99Y
sajajen=3

M.100.18

‘N.6S9'vz

‘Shey
рис!

‘AjuNoD

SOIN

(1621
‘инешо)

7175869)

PFSLBEEAV

2661
‘WWd
‘ay

‘e9eA
Аэу
‘uoygeleyy

JO
jes
yoyed
‘ul
/
:epuol4

"W'S'N

680ZZE

НМИ=

SMJESSN28p

‘Jo
зэроэвИц1

(‘1e6j8u1e die))
MESS‘:"2ZJ[1Hsз°SLLNWU0066еnELN2PP.'07ıщWрF W 8 6S218Toл оE'AG' 01bPоэSS 'N 9$iZщвE wLеSиOeW оцMnH / b s

022,
‘piepeno

зероэвиц1

VNGIS8Z

\машм

128\/10798[09

Ay12907

#
Boy

solsods

++'Y9u IeYg uss)

(penunuos)

10 GOLDING ET AL.

Annealing temperatures were optimized for
each primer pair combination and ranged from 48°C-55°C. A5 ul aliquot of each PCR product
was run out on a 1% agarose gel. When single
bands of the appropriate size resulted from
these amplifications, the PCR product was prepared for sequencing using Geneclean Ill (MP Bioproducts Inc.) or Qiagen’s QIA Quick PCR Purification Kit (Catalogue 28104). When supernumerary bands were present, the entire PCR product was run out on a 3% Nu-Sieve TAE agarose gel, the band of the correct size was excised under long wavelength ultraviolet light, and purified for sequencing following the protocols in Geneclean Ш (Catalogue 1001- 600). Purified PCR products were either cycle sequenced using BigDye 3.0/3.1 chemistry and analyzed on an АВ! 3100 genetic analyzer or sent off campus for sequencing at GeneWiz (New Jersey, U.S.A.; www.genewiz.com). In all cases, the DNA sequence of both strands was obtained before a final consensus sequence was generated for each taxon.

Data Editing and Phylogenetic Analyses

Given that a close caenogastropod sister-group has yet to be identified for the Vermeti-dae, outgroup selection remains problematic for this family. Recent studies (Colgan et al., 2007; Criscione & Ponder, 2012; Rawlings et al., unpublished data), in combination with the sperm morphological work of Healy (1988), however, support the evolution of vermetids from within the “lower” Hypsogastropoda, with possible ties to members of the Janthinoidea, Stromboidea, Calyptraeoidea, Xenophoroidea and Littorinoidea (Healy, 1988; Criscione & Ponder, 2012; Rawlings et al., unpublished data). In light ofthis, we chose representatives of two of these superfamilies, Littorina littorea (Littorinoidea) and Crepidula fornicata (Calyp-traeoidea) for rooting our phylogeny. DNA was extracted and amplified for the mtDNA regions for both outgroup taxa; 28S rRNA nucleotide sequences were obtained from NCBI. Because of substantial length differences in the amplified fragment of mtDNA across the taxa sampled, we first determined the comple-ment of genes present within these sequences. To begin, we searched all sequences for tRNA genes using tRNAscan-SE (Schattner et al., 2005), using the settings for mtDNA and the invertebrate genetic code. Once tRNA genes were identified, and their boundaries deter-mined, we used MacVector (MacVector, Inc.) to

find potential coding sequences of DNA in the intervening stretches of sequence, and BLAST (http://blast.ncbi.nim.nih.gov/Blast.cgi) to iden-tify these regions based on matches (in identity and length) of the derived amino acid sequence to homologous protein sequences from other gastropod mtDNAs. The start of coding se-quence was identified by a standard initiation codon (either ATG, ATA, or GTG). When pos-sible, the first proper stop codon (TAG or TAA) downstream of the initiation codon was chosen to terminate translation; however, to reduce overlap with downstream genes, abbreviated stop codons (T or TA) were selected in some instances. Ribosomal RNA sequences were also identified based on BLAST searches. The precise boundaries of rRNA genes, however, could not be determined due to the lack of sequence conservation at the 5’ and 3’ ends; therefore, the location of each rRNA gene was assumed to extend from the boundary of the upstream flanking gene to the boundary of the downstream flanking gene.
Once gene identities and boundaries were determined within the sequenced mtDNA fragment, we built gene specific datasets based on identified sequences of rrnS, trnV, and rrnL; other genes that were identified in amplification products of select taxa, including tRNA genes, trnK, trnP, trnE, trnLcyn, and the protein-encoding gene, nad6, were not used in subsequent phylogenetic analyses. Gene specific datasets of the mtdna genes (rrnS, trnV, rrnL) and the nuclear gene sequence (28S rRNA gene) were individually aligned using the online version of MAFFT (version 7; http://mafft.cbrc.jp/alignment/server/ref) using E-INS-i — an alignment method recommended for sequences with multiple conserved domains and long gaps — characteristics which typify rRNA genes. Because of uncertainty in several areas of the aligned rrnS and rrnL dataset as-sociated with length variation among taxa, we created two versions of these alignments: one which included all sites (“complete”) and one in which areas of poor alignment (as identified by eye and through confidence evaluation us-ing T-Coffee, Di Tommeso et al., 2011) were excluded (“pruned”). We employed JModelt-est2 (Darriba et al., 2012) to determine the best model of sequence evolution based on log likelihood ratio tests for each data parti-tion, and exclusion set, as determined using the Akaike Information Criterion. Because of the short length of the trnV gene (70-80 bp in length) sequence from this gene was combined

“DENDROPOMA GROUP” WORM-SNAILS 11

with the rrnS dataset for model evaluation in JModeltest2 and subsequent phylogenetic analyses. Alignments of all data sets were incorporated into one data file partitioned into three gene regions: (1) rrnS and trnV, (2) rrnL and (3) 28S rRNA; this was done for both the complete and pruned datasets.
Base compositional tests were implemented in PAUP* (Swofford, 2002) using chi-squared tests to ensure that there were no significant confounding differences in base composition across taxa. Parsimony-based phylogenetic analyses were also performed in PAUP*, with separate runs performed for each of the three data partitions and the combined dataset for both the pruned and complete alignment. Heuristic searches employed equal weighting of characters, TBR branch swapping, and 100 random sequence additions of taxa. Bootstrap analyses to determine branch support were undertaken using 1,000 pseudoreplicates. Phylogenetic analyses were also under-taken using Bayesian inference as employed in MrBayes (v3.2.1; Ronquist & Huelsenbeck, 2003). Evaluation of log likelihood ratio tests using the Akaike Information Criterion ranked the GTR + y + | model of molecular evolution as the best for all data partitions except for 28S rRNA, for which the TIM3 + y + | was ranked highest. Consequently, we applied model parameters “nst = 6, invgamma” to each data partition separately, and allowed parameters to vary independently for each partition. Default priors were used in all analyses. Posterior probabilities of phylogenetic trees were based on running 1.5-2x 106 generations of MCMC (depending on the dataset), which included two simultaneous runs of 4 chains (1 heated; h = 0.2) starting with a random tree and sampling every 100 generations. Preliminary runs of the data output in Tracer (Rambaut & Drummond, 2007) were used to determine the appropriate burn-in for the dataset and ensure stationar-ity of the dataset. In total, 1,000 trees (5-7% of the dataset) were excluded as burnin; the remaining 14,000-19,000 trees (depending on the dataset) were used to determine the 50% majority-rule consensus phylogram and estimate Bayesian posterior probabilities.

Synonymies/Chresonymies

Vermetid shells are notoriously difficult to identify and, even when accompanied by a photograph, published records often are not interpretable to specific level. We were thus

very selective in adding entries to our syn-onymy and chresonymy listings, limiting them to (1) those relevant to establishing available names and linking them to past monographs,
(2) material personally studied, and (3) clearly recognizable literature data (e.g., pointing to good photographs or other available data).

Terminology/Abbreviations

Protoconch sculpture is referred to as axial or spiral in the traditional sense, but because adult vermetids rarely coil around a defined axis, teleoconch sculpture is described as transverse (= axial) or longitudinal (= spiral). The reproductive system displayed many differences between taxa, but the function of individual components is not well understood. This study did not explore the function of the reproductive system, and simple terms have been used to avoid inferring function. The glan-dular, pallial section of the reproductive tract is simply referred to as the pallial oviduct or vas deferens and is open in all species examined. Structures containing sperm in the pallial ovi-duct are referred to as seminal receptacle(s), even if more than one is present.
The following abbreviations are used to label illustrated structures:
ag accessory gland
an anus
cm columellar muscle
co coelomic oviduct
cr cartilaginous rod
ct cephalic tentacle
cvd coelomic vas deferens
dv diverticulum of pallial oviduct
ec egg capsules
ep expanded distal pocket of pallial oviduct es esophagus
fg food groove
gi gill
hg hypobranchial gland
mo mouth
ms mantle slit
no notch in pallial oviduct
op operculum
os osphradium
оу ovary
ро раша! oviduct
pt pedal tentacle
pvd pallial vas deferens
re rectum
sr seminal receptacle
sv seminal vesicle
te testis

12 GOLDING ET AL.

The following abbreviations are used for institutions:
AM Australian Museum, Sydney, Australia
BPBM Bernice Pauahi Bishop Museum,
Honolulu, U.S.A.
FMNH Field Museum of Natural History, Chicago, U.S.A.
MNHNC Museo Nacional de Historia Natural de Chile, Santiago, Chile
MNHNP Museum National d’Histoire Naturelle, Paris, France
NHMUK Natural History Museum, London, United Kingdom
NMNZ Museum of New Zealand Te Papa . Tongarewa, Wellington
QM Queensland Museum, Brisbane,
Australia
UF Florida Museum of Natural History,
Tallahassee, Florida, U.S.A.
WAM Western Australian Museum, Perth,
Australia
ZMC Zoologisk Museum, Copenhagen,
Denmark

RESULTS

Molecular Data

PCR amplifications were successful for all target taxa and genes except in two instances. For Dendropoma mejillonense, we were only able to amplify a small 5’ portion (rrnS) of the mtDNA target region, approximately 400 bp in length, and were unsuccessful in amplify-ing the remaining downstream region even with different primer combinations, annealing temperatures, and increased MgCl, concentra-tions. In addition, we were unable to amplify the 28S rRNA gene for Cupolaconcha sp. (FMNH 302015). Both taxa were still included in our phylogenetic analyses even though their data-sets were not complete.
PCR amplification lengths of our mtDNA data-set were indicative of gene order changes that have occurred within the vermetid mt genome and have been described partly elsewhere (Rawlings et al., 2001, 2010). Dendropoma corrodens, D. nebulosum, D. platypus, D. gre-garium, D. cf. petraeum, D. rhyssoconchum and D. psarocephalum, were all were found to share an indel consisting of trnk, trnP and nad6 posi-tioned between rrnS and trnV, relative to other taxa sampled. Given that D. mejillonense was nested within this clade, it is assumed that this taxon also shared this gene rearrangement, al-

though we were not able to confirm this directly for the reasons described above. Members of the genus Cupolaconcha were also unique in lacking trnV between the rrnS and rmL. Align-ments with other taxa across the rrnS-trnV-rrnL region invariably resulted in a long gap in this region for Cupolaconcha suggesting that its trnV has been translocated to another region of the genome. Thylaeodus also presented a novel gene arrangement. For this taxon, an additional trnE was located between trnV and rrnL (Rawl-ings et al., 2010). Thylacodes squamigerus also exhibited a gene rearrangement in this region involving the presence of rrnS, rrnL and nad1 pseudogenes, an extra trnV and trnL yy (Rawl-ings et al., 2010). For all other taxa included in our dataset, the standard gene order of rrnS-trnV-rrnL was present.
Gene-specific alignments were 618 bp, 78 bp, 1,577 bp and 1,123 bp in length for the rms, trnV, rrnL, and 28S rRNA gene regions, respectively, and 696 bp for the combined rrnS + trnV dataset. The complete dataset thus con-sisted of 3,396 characters, of which 1,494 were parsimony informative. The pruned dataset for the rrnS + trnV partition was 530 bp in length, 166 bp shorter than the complete alignment, while the pruned rrnL dataset was 737 bp in length, over 50% shorter. In total, the combined pruned dataset consisted of 2,390 characters, of which 765 were parsimony informative. Base compositional tests were not significant across taxa for the pruned mtdna datasets or the 28S rRNA dataset, but significant differences in base composition were evident in the complete rrnL dataset (x2 = 392.5, df = 105, P = 0.00). These differences did not persist in the pruned rrnL dataset (x2 = 92.9, df = 105, P = 0.79), in-dicating that these differences were confined to regions of poor alignment typically associated with sequence length variation across taxa.

Phylogenetic Analyses

The overall pattern of relationships among taxa was largely consistent across data parti-tions, pruned/complete datasets, and methods of analysis (Parsimony, Bayesian), with relative-ly few exceptions (Table 2). For clarity, we have presented only the 50% majority rule consensus phylogeny based on a Bayesian analysis of the combined rrnS + trnV, rrnL, and 28S rRNA pruned dataset with posterior probability values (where > 95%) and parsimony-based bootstrap values (where > 70%) mapped onto their ap-propriate clades (Fig. 6). Disagreements in the

“DENDROPOMA GROUP” WORM-SNAILS 13

TABLE 2. Clade support values (PP/BP, in %) resulting from Bayesian and Parsimony-based phyloge-netic analyses of individual and combined gene regions using the pruned dataset.

Ce+enrdareospiogmnau m
DC+ ernadersoipgonmuam

©

5 5
$ S
g E
Dataset Q > Q

rns + trnV 97/50-::<50/52 1100/1400
rrnL 100/77 80/54 100/100
All mtDNA 100/93 62/70 100/100
All mtDNA + 28S rRNA 100/96 56/62 100/100

Clade

+

+ 3
о © о ©
$ со $ =
Е В

= LS MURS ©
D USE us ©

= ие + = Е ++ £+ £ = фо оф о

5 © ве S

© © ac? ae Е.
® 75) AIO (ab) AS) Y © SV
© © © US о © ©

EE er Je. O = ORR OR о
100/78 100/94 < 50/< 50 100/93 100/64 100/92 100/99 100/51 98/<50 100/91 100/95 100/100 100/51 100/82 100/99 100/95 100/100 98/<50 100/86 100/100

results of different data partitions are largely re-flected in those major clades with low posterior probability and bootstrap values (Table 2). Analyses of our molecular dataset, us-ing both parsimony and Bayesian methods, supported a phylogeny consistent with the new taxonomic framework for “Dendropoma group” taxa proposed herein. This was true for both the complete dataset and the pruned dataset, which excluded poorly aligned re-gions across data partitions. Each of the four genera, Dendropoma, Ceraesignum n. gen., Novastoa and Cupolaconcha n. gen., formed a strongly supported monophyletic grouping (Fig. 6). High bootstrap (96%) and posterior probability (100%) values also supported the placement of Dendropoma, Ceraesignum n. gen., and Novastoa, within their own clade, separate and distinct from members of the genus Cupolaconcha n. gen. (Table 2). Strong genetic differentiation among members of Den-dropoma, Ceraesignum п. gen., and Novastoa, as represented by long branch lengths in Figure 6, and morphological differences (see below) were also consistent with recognition of these three groups at the generic level. Members of the genus Dendropoma were also defined by a novel pattern of mtDNA genes (rrnS-trnK-trnP-nad6-trnV-rrnL) not found in Ceraesignum and Novastoa. There was no strong evidence of

a hierarchical pattern of relationships among these three genera, however: both Bayesian and parsimony analyses of the pruned dataset weakly supported a sister group relationship between Dendropoma and Ceraesignum, but this pattern was not consistent across data partitions and analyses (Table 2).
Species of Cupolaconcha n. gen., in turn, were found to be more closely related to mem-bers of the vermetid genera, Petaloconchus, Thylaeodus, and Eualetes, than to Dendro-poma, Ceraesignum n. gen., and Novastoa. The translocation of trnV evident in Cupola-concha n. gen. mtdna, however, was confined to this genus alone and was not observed in any members of its sister clade. Thylacodes and Vermetus were strongly supported as closely related to the Cupolaconcha n. gen., Eualetes, Petaloconchus, and Thylaeodus clade in Bayesian analyses of the pruned and complete dataset, but not in parsimony-based results and isolated gene partitions (Table 2). In these analyses, one or both of these genera were more closely allied to the Dendropoma, Ceraesignum n. gen., Novastoa clade or al-ternatively no strong support was shown for a relationship with either clade.
High levels of genetic differentiation were observed within genera and nominal species of vermetids sampled in our analysis. Within

14

D. corrodens, for instance, taxa differed up to 18% (uncorr.-P) in nucleotide sequence based
on our mtDNA dataset, with 15% difference recorded between two specimens collected from Barbados. Such high levels of genetic differentiation hint of cryptic species residing

/731
Barbados 1
*/76

95

„Jordan
* ey *

*

Cook Islands

GOLDING ET AL.

within this grouping and highlight the need for further study of D. corrodens. Within genera, sequence divergence levels in mtDNA exceed-
ed 30% (uncorr.-P) in pairwise comparisons of
taxa within Dendropoma, Ceraesignum n. gen., and Cupolaconcha n. gen.

Florida
Belize

iy Le Dendropoma cf. corrodens British Virgin Isl. 2
British Virgin Isl. 1
Barbados 2
Dendropoma gregarium
Dendropoma psarocephalum
Dendropoma platypus
Dendropoma rhyssoconchum
Dendropoma mejillonense
Dendropoma cf. petraeum
а Florida
"Lu Bahamas

Dendropoma nebulosum

Ceraesignum maximum

Ceraesignum robinsoncrusoei п. sp. Novastoa caboverdensis п. sp.
Novastoa bahamensis п. sp.
- Novastoa pholetor n. sp. Novastoa sp.

*

99

98

99

*
*

Hawaii
| Cupolaconcha meroclista Mariana Islands
Cupolaconcha sp.
Belize
«|L British Virgin Islands
* "L Bahamas Eualetes tulipa

Cupolaconcha guana n. sp.

Petaloconchus varians
Petaloconchus montereyensis
Thylaeodus sp.
Thylacodes squamigerus
Thylacodes cf. decussatus

+

Vermetus triquetrus
Vermetus cf. triquetrus
Crepidula fornicata
Littorina littorea
0.2

FIG. 6. Phylogenetic relationships among Dendropoma, Ceraesignum, Novastoa, and Cupolaconcha and other select vermetid genera, using Littorina littorea and Crepidula fornicata as outgroups. The phylogram illustrated represents the 50% majority-rule consensus tree from a Bayesian analysis of the combined gene (rrnS, trnV, rrnL, and 28S rRNA genes), pruned alignment, dataset based on a sampling of 19,001 trees (2,000,000 generations, sample frequency = 100, burnin = 1,000, heat = 0.2). Support values for clades are posterior probabilities (where 2 95%, above branches) from the Bayesian analysis and bootstrap percentages (where 2 70%; below branches) from a parsimony-based analysis of the same dataset (1,000 pseudoreplicates). Asterisks represent support values of 100%.

“DENDROPOMA GROUP” WORM-SNAILS 19

SYSTEMATIC PART

Assessment of Genus-Group Names Previously Used in the Dendropoma Group

Species now considered as belonging to Dendropoma sensu lato have been introduced, or subsequently placed, in a bewildering variety of genus-group names, some of which are now known ort hought to belong to polychaete worm groups whereas others are technically unavail-able for nomenclatural reasons. Because the current study finds the clade diversity in Den-dropoma s.l. greater than previously expected, it will be necessary to analyze the availability of generic names in this complex. Keen (1961) assembled a list of assumed synonyms and subgenera of Dendropoma, which were further analyzed for availability — in the sense of the 1.Z.C.N. [1999] Code — by Bieler & Petit (2011). Expanding on these works we find:

(1) Names that are invalid and cannot be used:

Siphonium “Browne, 1756”

Siphonium “Browne, 1756”, is a pre-Linnean name included in the synonymy of Vermetus by Gray (1847: 156) but not made available thereby under 1.C.Z.N. (1999) Art. 11.5.2. It was also cited as of Browne, sometimes in a slightly different sense in Vermetidae, by numerous authors (e.g., H. Adams & A. Adams, 1854: 356-357; Cossmann, 1912: 134). Gray (1850:
82) can be credited with a formal introduction of the name (type species not designated), but Siphonium Gray, 1850, is invalid because preoccupied by Siphonium Link, 1807 [Ce-phalopoda]. For additional discussion of the name Siphonium, see Keen (1980).

Spiroglyphus Daudin, 1800

Spiroglyphus Daudin, 1800, was introduced (1800: 39) with two nominal species, Spirogly-phus politus Daudin, 1800, and Spiroglyphus annulatus Daudin, 1800. The name has been widely used since the 1840s as a molluscan genus and mostly applied to entrenching vermetids in today’s concept of Dendropoma. Hartman (1959: 47) included Spiroglyphus in her list of possible polychaete annelid genera. Keen (1961: 184, 191) stated that the included species “should probably classed as annelids” and for Spiroglyphus it is “advisable to set it aside as a genus dubium”; and subsequently (Keen, 1980; Keen & Hadfield, 1985) sought

suppression of the name under I.C.Z.N. rules. Spiroglyphus was placed on the Official Index of Rejected and Invalid Generic Names in Zool-ogy in Opinion 1425 (1.C.Z.N., 1987).

Bivonia Gray, 1842

After describing the genus in 1842 (p. 90), Gray first provided a type species in 1847 (p. 156), Vermetus glomeratus Bivona-Bernardi, 1832 — a nominal species later renamed as Bivonia petraea Monterosato, 1884 (= Dendro-poma petraeum herein). Gray’s name is invalid because it is preoccupied by Bivonia Cocco, 1832 [Crustacea]. lt has, however, remained in use until very recently for vermetid taxa (e.g., Bielokrys, 1999). Anominal species described as Bivonia exserta Dall, 1881, is discussed below, and its type specimen shown to be a polychaete worm.

Stoa de Seres, 1855

Stoa de Serres, 1855, was introduced (1855:
238) with three new species, Stoa ammoniti-formis, S. spiruliformis and S. perforans, without any subsequent type designation. It was consid-ered a synonym of Spiroglyphus or subgenus of Siphonium in Vermetidae by Mörch (e.g., 1862: 326), and largely fell into disuse. Keen (1961:
184) suggested that Stoa species were annelids and subsequently (Keen & Hadfield, 1985) pro-posed that the name Stoa be suppressed under 1.C.Z.N. powers. 1.C.Z.N. Opinion 1425 (1987) placed it on the Official Index of Rejected and Invalid Generic Names, suppressing it for the purposes of the Principle of Priority but not for those of the Principle of Homonymy.

(2) Names previously considered synonymous but considered incertae sedis herein:

Magilina Vélain, 1877

First listed by Vélain (1876: 285) as a no-men nudum, Magilina was formally introduced in the following year (1877: 105-106) based on Magilina serpuliformis Vélain, 1877 (1877: 106-107, figs. 16-18), and an unnamed Miocene species. Magilina serpuliformis was described and illustrated as an extremely small-shelled species, with the adult shells measuring 3 to 4 mm in height and 1.25 mm in diameter. Keen (1961: 198) placed the nominal genus in tentative synonymy with Dendropoma. How-ever, the original description and illustration of a very small shell with long upright feeding

16 GOLDING ET AL.

tube and a glossy and smooth protoconch do
not match the conditions of the species treated
herein. Magilina remains incertae sedis until
type material can be investigated.

Vermitoma Kuroda, 1928

The genus-group name and its type (and only included) species Vermitoma luchuana Kuroda, 1928, was introduced in a catalog work by Kuroda (1928: 40) who credited the names to a manuscript by Hirase. The species was subsequently placed in Dendropoma by vari-ous authors (e.g., Hasegawa in Okutani, 2000: 207), an action that synonymizes Vermitoma under Dendropoma. However, the original de-scription of V. luchuana by Kuroda (1928: 40, footnote in Japanese) described features that do not support this interpretation. Kuroda men-tioned that the living specimen does not show affinities with either vermetids or siliquariids, and in particular referred to a scissurellid-like shell slit that was being filled in as growth pro-ceeded but remained open as an elongated oval hole near the aperture. Vermitoma thus also remains incertae sedis until type material can be investigated.

(3) Name based on an Upper Oligocene fossil species in need of further investigation:

Elliptovermetus Cossmann & Peyrot, 1922, was introduced by its authors (1922: 69) with its type species by original designation, Ver-metus breigneti Cossmann & Peyrot, 1922, from Aquitanian fossil beds [Early Miocene] of France. The description and figure of the type species depict a tube that is ovate in cross-section, deeply immersed in coral, and showing lamellar growth striae and a raised mid-dorsal crest. Keen (1961: 200) considered it a subge-nus of Dendropoma. No extant species have been linked to this taxon.

(4) Three available names that can be applied to extant taxa in this group:

Dendropoma Mörch, 1861

Mörch (1861: 153) introduced the genus as a “section” of Siphonium. Type species, by subsequent designation of Keen (1961: 189), is Siphonium (Dendropoma) lituella Mörch, 1861, from California. The genus name was placed on the Official List in Opinion 1425 (1.C.Z.N., 1987).

Novastoa Finlay, 1926

Finlay (1926: 386) based his new genus on the type species, by original designation, Siphonium lamellosum Hutton, 1873, from New Zealand.

Veristoa lredale, 1937

Iredale (1937: 254) based Veristoa, by origi-nal designation, on Veristoa howensis lredale, 1937, from the Tasman Sea.

Few formal attempts have been made to subdivide Dendropoma in a systematic man-ner. Early arrangements (e.g., Mörch, 1860) separated large and solitary forms into “Si-phonium” and “Bivonia,” respectively. One hundred years later, Keen (1961: 193-199) similarly recognized two subgenera for the extant species, Dendropoma s.s. (for “mainly solitary forms, minute to large”) and Novastoa (for “colonial forms, usually encrusting rocks in honeycomb-like sheets”). Keen (1961: 200) expressed uncertainty about the validity of this taxonomic distinction based on growth habit, stating in her treatment of Novastoa that this “group may be only situs forms, not a true ge-netic unit, for specimens in the dense clumps may be, to the eye, indistinguishable from solitary specimens as to operculum, nuclear whorls, and sculpture.” As will be shown below, the type species of Dendropoma and Novastoa indeed belong to different clades, although it is not the distinction of solitary versus gregarious life mode that distinguishes them.
Based on analyses of shell morphological and anatomical characters, the studied taxa of the Dendropoma group fall into four separate units, here considered genera. The following section describes and arranges 21 species (eight of which are new) into four genera: Dendropoma (with Veristoa in synonymy), Novastoa, Ceraesignum n. gen., and Cu-polaconcha n. gen. Additional species, not morphologically studied in detail, are assigned to these groups based on literature and/or molecular data.

TAXON DESCRIPTIONS

Gastropoda
Caenogastropoda
Vermetoidea Rafinesque, 1815
Vermetidae Rafinesque, 1815

“DENDROPOMA GROUP” WORM-SNAILS 17

Dendropoma Mörch, 1861

Dendropoma Mörch, 1861: 153 [placed on the Official Lists of Generic Names in Zoology by 1.C.Z.N. (1987)].
Spiroglyphus of authors, not of Daudin, 1800 [the latter placed on the Official Index of Rejected and Invalid Names in Zoology; ICZN (1987)]. Stoa of authors, not of Daudin, 1800 [the latter placed on the Official Index of Rejected and Invalid Names in Zoology; ICZN (1987)]. Veristoa lredale, 1937: 254. With type species, by original designation, Veristoa howensis Iredale, 1937 (see below).

Type Species

Siphonium (Dendropoma) lituella Mórch, 1861, by subsequent designation of Keen (1961: 189).

Diagnostic Description

Teleoconch: Small to medium (maximum di-mension 6-40 mm), “tube” narrow or wide (apertural diameter 1.6-11.4 mm), without expanded chamber behind aperture; whorl coiling pattern concentric but sometimes tending to “Turritella-squeezed-sideways”, either shallowly entrenched in substratum or spiraling vertically through aggregate matrix (composed of conspecific shells); aperture either flush with substratum/aggregate matrix or forming feeding tube above substratum/ag-gregate matrix; scars from abandoned feeding tubes sometimes present; often encrusted with epifauna. Shell thick; aperture simple. Color variable, sculpture of tall or low transverse lamellae, with or without longitudinal crests/ ridges/carinae. Interior surface color variable; sculpture on columellar surface absent; con-cave septa frequent in abandoned shell.

Protoconch: Settled/hatchling protoconch diameter 410-950 um, height 360-860 um. Strong “hook” projection present on apertural lip. Intracapsular growth only evident in proto-conch structure; globular with large increase in whorl size; moderately deep suture; 1.3 whorls; sculpture variable; spiral keel(s) at base of whorl absent or present. Color vari-able, transparent.

Operculum: Circular in axial profile; diameter proportional to shell size, 1.0-7.7 mm. Com-posed of chitin only; color variable. Varying

between conical with concave exterior sur-face, and “mushroom-shaped” with domed, convex exterior surface. Exterior surface with spiral lamina pressed flat, appearing “stacked” on “mushroom-shaped” opercula; usually en-crusted with epifauna. Interior surface either concave or convex, with prominent mammilla conical to nipple-shaped; peripheral surface smooth and glossy; muscle attachment area textured with shallow concentric grooves.

Radula: Taenioglossate, transparent, color-less. Length of ribbon 1.0-2.9 mm; 34-53 rows (proportional to shell size). Trapezoidal rachidian tooth with prominent central cusp flanked on each side by three smaller cusps decreasing in size outwardly. Base of lateral tooth notched to interlock with rachidian and inner marginal teeth; elongate main cusp flanked by 1-2 cusps on inner side, 2-3 cusps on outer side (variable within a population). Inner marginal tooth slender with one cusp on inner side, 2-3 cusps on outer side. Outer marginal tooth smooth on outer side, one or 2-3 cusps on inner side; base simple, without projection.

External Morphology and Color. Body of animal usually stout (length 35 mm), occupying be-tween 1.5 and 3 last whorls ofs hell; 0.5x body length composed of gonad and digestive gland. Columellar muscle moderately long, extending between 0.5 and one whorl. Pedal tentacles short (in preserved specimens). Head relatively large, cephalic tentacles short (in preserved specimens), broad, with tiny ommatophore bearing eye at outer base; right side of head with food groove with simple margins. Adult male and female mantle undi-vided. External body coloration variable.

Pallial and Reproductive Anatomy: Gill 0.2x mantle width, full length of mantle cavity; gill leaflets medium height to tall triangular; 13-22 leaflets per mm. Osphradium short to moderately long relative to mantle cavity, 1.1-5.3 mm long; margins smooth; anterior tip straight or curved towards columellar muscle. Rectum running straight or kinked from coelom to anterior right mantle cavity; fecal pellets cigar shaped. Hypobranchial gland pale brown, covering surface of mantle between gill and rectum, sometimes also covering rectum and pallial oviduct. Раша! oviduct notched near midpoint, sometimes with expanded pocket distal to notch; proxi-

18 GOLDING ET AL.

mal diverticulum sometimes present. Primary
and accessory seminal receptacles present,
attached to base of proximal oviduct via short
duct. Male reproductive system with notch
near base of pallial vas deferens; accessory
gland present in exhalant channel near an-terior tip of pallial vas deferens.

Development and Ecology: 3-8 unstalked egg capsules held in female mantle cavity; double-walled capsule semi-transparent, round to ovoid, diameter increasing with development of embryos; number of eggs/ embryos per capsule varying between spe-cies. Larval biology with direct development or short planktonic phase. Adults solitary to gregarious or reef-building.

Comparative Remarks

All known species of Dendropoma s.s. pro-duce unstalked egg capsules and brood them in the mantle cavity (females lack a pallial slit) rather than attaching the capsules to the shell wall as in the other vermetid genera examined here. This reproductive strategy is unusual in

Vermetidae, but it has been reported in Peta-loconchus montereyensis Dall, 1919 (Hadfield, 1970, 1989), and in two nominal species of Vermetus. The latter — studied as Vermetus alii Hadfield & Kay, 1972, by Hadfield et al. (1972) from Hawaii and as Vermetus sp. by Miloslavich & Penchaszadeh (1992) from Panama - are here both considered as belong-ing to Eualetes tulipa (Chenu, 1843), based on detailed morphological and molecular compari-sons to be published in different context. The habit of retaining egg capsules inside the unslit female mantle therefore cannot be considered a unique synapomorphy of Dendropoma $3. $. However, it is unique to Dendropoma s.s. among the group of vermetids examined in this study and is a particularly useful charac-ter for differentiating the genus as a subset of the “Dendropoma group”. Petaloconchus montereyensis and E. tulipa are dissimilar to Dendropoma s.s. in many other regards, and
could not be confused with Dendropoma s.s. on
the basis of reproductive strategy alone.
The Dendropoma operculum has two distinct
forms: flat to conical with a concave exterior
surface, or “mushroom-shaped” with a convex

FIG. 7. Distribution map of Dendropoma Mörch, 1861 based on material examined in this study. Filled diamond = D. lituella (Mörch, 1861); hollow diamond = D. mejillonense Pacheco & Laudien, 2008; filled square = D. nebulosum (Dillwyn, 1817); hollow square = D. platypus (Mörch, 1861); filled triangle = D. cf. petraeum (Monterosato, 1884); hollow triangle = D. cf. corrodens (d’Orbigny, 1841); filled star = D. gregarium Hadfield & Kay, 1972; hollow star = D. howense (Iredale, 1937); filled cross = D. cf. tholia Keen & Morton, 1960; hollow cross = D. expolitum n. sp.

“DENDROPOMA GROUP” WORM-SNAILS 19

exterior surface. The operculum fills the aper-ture of the shell but does not have a raised, ruffled lamina on the exterior surface, as in Novastoa. The lamina on the operculum of Dendropoma is multispiral, but is pressed flat when the operculum is concave conical (except in D. platypus, where it is sometimes raised for a single revolution) or “stacked” (comprising many horizontal layers) when the operculum is “mushroom-shaped”.
The reproductive system also displays some unique characters. For example, the male pallial genital tract is connected to an acces-sory glandular patch in the exhalant channel, of unknown function but perhaps related to spermatophore production.

Taxonomic Remarks

Dendropoma forms a well-supported, mono-phyletic clade in the molecular phylogenetic analysis (Fig. 6). Although there are two sub-clades in Dendropoma, we have not introduced subgeneric divisions into the classification. The two subclades approximately correspond to the two different operculum forms, however D. petraeum has an intermediate (flat) oper-culum and is allied with the conical, concave operculate taxa in the molecular phylogeny. These informal groups are referred to here as “concave-operculate” and “convex-operculate” groups. The following systematic descriptions address species belonging to the “concave-

operculate” group first, followed by species belonging to the “convex-operculate” group.

Diversity and Distribution (Fig. 7)

Ten species are examined here and included in Dendropoma s.s. Only one taxon, from northern Australia, is newly described. There are many other available names in the literature attributed to Dendropoma and others that were described in different nominal genera but likely belong here (Bieler & Petit, 2011), but most are poorly described and cannot be placed in this genus with any certainty. Spiroglyphus stramonitae Mörch, 1862, originally described from two apparently juvenile specimens and uncertain locality (“Ситеа?”), is here consid-ered a member of Dendropoma s.s. (Figs. 8, 9). Dendropoma psarocephalum Hadfield & Kay, 1972 (Hawaii), and Dendropoma rhysso-conchum Hadfield & Kay, 1972 (Hawaii), were included in the molecular phylogenetic analy-sis, and their generic placement is confirmed. Several other species, for which adequate descriptions and figures are available in the literature, appear to belong in Dendropoma s.s. but were not examined in this study, including: Dendropoma marchadi Keen & Morton, 1960
(Senegal), Dendropoma ghanaense Keen &
Morton, 1960 (Ghana), Dendropoma squam-
iferum Ponder, 1967 (New Zealand), and Bivo-
nia dragonella Okutani & Habe, 1975 (Japan;
based on redescription by Ekawa & Sakashita,

FIGS. 8, 9. The two syntypes of Spiroglyphus stramonitae Mörch, 1862, a nominal species described from uncertain type locality given as “Guinea?”; here interpreted as belonging to Dendropoma s.s. ZMC GAS-228. FIG. 8: Syntypes on shell of muricid gastropod Stramonita haemastoma (Linnaeus, 1767), largest diameter of both type specimens = 3.0 mm; FIG. 9: Internal (left) and external aspects of single, damaged operculum in this type lot. ZMC GAS-228. Scale bar = 500 um.

20 GOLDING ET AL.

2013). Crucially, the available descriptions of
the above species include detailed accounts
of the operculum and the animal, permitting confirmation of key features distinguishing Den-
dropoma s.s. from Novastoa, Ceraesignum п.
gen. and Cupolaconcha n. gen. In most cases, shell characters alone are uninformative for generic assignment.
Dendropoma spp. are distributed globally in tropical and temperate waters. Two nominal species (at least one of which appears to be a species complex) occur sympatrically in the Caribbean.

Dendropoma lituella
(Mörch, 1861)

Siphonium (Dendropoma) lituella Mörch, 1861: 154-155 [placed on the Official List of Specific Names in Zoology by Opinion 1425 (1.C.Z.N. 1987)]; Bieler & Petit, 2011: 44. Dendropoma (Dendropoma) lituella — Keen,
1961: 199, 206, text-figs. 26-29, pl. 55, fig.
1 [with selection and illustration of lectotype;
Morton, 1965: 588.
Spiroglyphus lituellus [sic] — Abbott, 1974: 100.
Dendropoma lituella - Keen, 1983: 10.

FIGS. 10-20. Dendropoma lituella (Mörch, 1861). FMNH 1689, San Diego, U.S.A. FIG. 10: A cluster of specimens removed from substratum. Scale bar = 10 mm; FIG. 11: Individual shell. Scale bar = 2 mm; FIG. 12: SEM image of teleoconch sculpture. Scale bar = 500 um; FIGS. 13, 14: Protoconchs removed from recently settled juveniles. Scale bar = 200 um. FIG. 13: Apical view; FIG. 14: Abapertural view; FIGS. 15-17: Operculum. Scale bar = 500 um. FIG. 15: Exterior surface; FIG. 16: Lateral view; FIG. 17: Interior surface; FIG. 18: SEM image of exterior surface of operculum. Scale bar = 200 um; FIG. 19: SEM image of interior surface of operculum. Scale bar = 200 um; FIG. 20: Central section of radula. Scale bar = 50 um.

“DENDROPOMA GROUP” WORM-SNAILS 24

21

FIGS. 21, 22. Anatomy of Dendropoma lituella (Mörch, 1861), based on a partial dried specimen that has been rehydrated. FMNH 1689, San Diego, U.S.A. Scale bars = 1 mm. FIG. 21: Right view of head; FIG. 22: Mantle cavity.

Type Locality

California, imbedded in a Haliotis shell; pre-
cise locality not known.

Material Examined

Lectotype and paralectotypes: NHMUK 195917. California, U.S.A.: FMNH 1689: San Diego, purchased from Ward’s Natural Science Est., October 1893, dry (many).

Description

Teleoconch (Figs. 10-12): Apertural diameter to 4.1 mm; shell length to 17 mm; diameter of last whorl to 9 mm. Up to four whorls coiled concentrically or slightly off center (*T urritella-squeezed-sideways”); shallowly entrenched in substratum; aperture flush with substratum; scars from abandoned feeding tubes absent. Exterior surface cream, with interior surface color faintly showing through; sculpture of low, scale-like transverse lamellae, crossed by longitudinal rib on dorsal surface flanked by 1-2 pairs of smaller ribs on each side. Interior surface cream on ventral surface, dark brown on dorsal surface.

Protoconch (Figs. 13, 14): Settled protoconch diameter to 840 um, height to 730 um.

Sculpture absent on first whorl, last 0.3 whorl with sculpture of shallow craters, roughly arranged in axial stripes; spiral keel absent. Honey brown.

Operculum (Figs. 15-19): Diametert o 2.7 mm. Shallow conical; opaque pale orange around muscle attachment area, transparent golden peripherally, with ring of dark orange at mar-gin. Lamina on exterior surface flat. Interior surface with low, nipple-shaped mammilla.

Radula (Fig. 20): Length of ribbon 1.2 mm; up to 34 rows. Outer marginal tooth: 2 cusps on ‚inner side.

External Morphology and Color (Fig. 21): Ob-servations of rehydrated specimens: Body occupying at least three whorls of shell. Dorsal surface of head gray, snout pale gray; cephalic tentacles pale gray with dark speckles; foot pale gray; mantle cream with diffuse gray behind anterior margin.

Pallial and Reproductive Anatomy (Fig. 22): Observations of rehydrated specimens: Os-phradium moderately long, anterior tip curved towards columellar muscle. Rectum straight.

Development and Ecology: Egg capsules not observed. Adults gregarious.

22 GOLDING ET AL.

Comparative Remarks

Belonging to a group of “concave-operculate” Dendropoma (D. lituella, D. mejillonense, D. nebulosum, D. platypus, D. cf. petraeum and
D. rhyssoconchum). Similar to other species
in this group with longitudinal sculpture, in par-ticular D. nebulosum, which also forms carinae from the transverse lamellae. Distinguished by the unique protoconch sculpture of craters arranged into axial bands.

Taxonomic Remarks

The examined specimens match well with the figured lectotype (Keen, 1961), but are growing more densely and are slightly larger. The shell and operculum match well with Keen’s (1961) description. The name lituella is a diminutive of lituus, a Latin noun referring to a cavalry
trumpet ог an augur’s staff used for divination,
and apparently describes the snail’s coiling
pattern. It is a noun in apposition.

23 25

28

FIGS. 23-32. Dendropoma mejillonense Pacheco & Laudien, 2008. FIG. 23: A cluster of specimens removed from the substratum, including lectotype (FMNH 329358, labeled with an asterisk). Paralec-totypes, ЕММН 312172, Peninsula Mejillones, Chile. Scale bar = 10 mm; Fig. 24: Lectotype (FMNH 329358, labeled with an asterisk) and several other specimens surrounded by numerous recently settled juveniles. Paralectotypes FMNH 312172, Peninsula Mejillones, Chile. Scale bar = 5 mm; FIG. 25: SEM image of teleoconch sculpture. FMNH 312173, Peninsula Mejillones, Chile. Scale bar = 500 um; FIGS. 26, 27: Protoconchs removed from recently settled juveniles. FMNH 312173, Peninsula Meiillones, Chile. Scale bar = 100 um. FIG. 26: Abapertural view; FIG. 27: Apical view; FIGS. 28-30: Operculum. FMNH 312173, Peninsula Mejillones, Chile. Scale bar = 1 mm. FIG. 28: Exterior surface; FIG. 29: Lateral view; FIG. 30: Interior surface; FIG. 31: SEM of exterior surface of operculum. FMNH 312173, Peninsula Mejillones, Chile. Scale bar = 100 um; FIG. 32: Central section of radula. FMNH 312173, Peninsula Mejillones, Chile. Scale bar = 50 um.

“DENDROPOMA GROUP” WORM-SNAILS 23

Distribution (Fig. 7)

Examined material from one location (San Diego, California, U.S.A). Distributed from southern California to the southern end of the Gulf of California at La Paz, Baja California (Keen, 1971b: 408).

Dendropoma mejillonense
Pacheco & Laudien, 2008

Dendropoma mejillonensis [sic] Pacheco & Laudien, 2008: 219-224, figs. 2, 3; Bieler & Petit, 2011: 46.

Type Locality

17 m, rocky vertical wall known as “Anemones Wall,” Peninsula Mejillones, Chile: 23.4695°S, 70.6190°W.

Material Examined

Chile: All from original syntypes: Lectotype: des-ignated herein (Figs. 23, 24), FMNH 329358: coll. by А. Pacheco, July 11, 2006, 70% EtOH (1 specimen attached to paralectotypes); Paralectotypes: FMNH 312172: 70% EtOH (many, attached to lectotype); FMNH 312173: 70% EtOH (many) [DNA sequence data].

Description

Teleoconch (Figs. 23-25): Apertural diameter to 4.5 mm (average 4.29 mm; Pacheco & Laudien, 2008); shell length to 20 mm; diameter of last whorl to 11.5 mm. Initial 2 whorls coiled concentrically, subsequent 1—2 whorls off-center; shallowly entrenched in substratum; aperture sometimes raised 1 cm above substratum as feeding tube; scars from abandoned feeding tubes occasion-ally present. Exterior surface chalky white to cream; sculpture of low, indistinct transverse lamellae without longitudinal ridges. Interior surface cream on ventral surface, pale fawn on dorsal surface.

Protoconch (Figs. 26, 27): Settled protoconch diameter to 950 um (770 um, according to Pacheco & Laudien, 2008); height to 860 um. Sculpture on all whorls of short, irregularly-shaped “gouge-marks” arranged in roughly spiral bands; spiral keel absent. Pale brown.

Operculum (Figs. 28-31): Diameter to 2.5 mm (average 2.7 mm, according to Pacheco & Laudien, 2008). Shallow conical; opaque reddish-orange around muscle attachment area, transparent golden peripherally. Lamina on exterior surface flat. Interior surface with low, nipple-shaped mammilla.

Radula (Fig. 32): Length of ribbon 2.1 mm; up to 52 rows. Outer marginal tooth: 1 cusp on inner side.

External Morphology and Color (Fig. 33): Body length to 25 mm (average 18 mm according to Pacheco and Laudien, 2008), occupying 2-3 whorls of shell. Columellar muscle ex-tending for 0.5 whorl. Color in life (modified from Pacheco & Laudien, 2008): Head pale grey to reddish with black, white and yellow speckles; foot pale orange with white band around operculum; cephalic tentacles brown or pale gray with black and yellow speckles and distinctive white stripe across base; pedal tentacles pale gray with yellow speckles; mantle pale orange with pale brown band on mantle edge. Color of specimens preserved in 70% EtOH: head-foot and mantle cream to pale gray with scattered black pigment on dorsal surface of head and sides of foot; cephalic tentacles pale gray with white then black stripes at base.

Pallial and Reproductive Anatomy (Figs. 34-37): Gill with 18 leaflets per mm; leaflets medium-height, triangular, breadth equal to height. Osphradium short, 2 mm long; ante-rior tip curved towards columellar muscle. Rectum straight. Hypobranchial gland ex-tending across rectum and proximal pallial oviduct. Pallial oviduct without expanded distal pocket or proximal diverticulum.

Development and Ecology (Fig. 38): 3-4 unstalked egg capsules per female; 3-10 embryos per capsule (Pacheco & Laudien, 2008). Larval biology not known, but intra-capsular larval shells same size as settled protoconchs, suggesting direct development. Adults gregarious.

Comparative Remarks

Similar to other “concave-operculate” Den-dropoma species, but with weak transverse lamellae and without any longitudinal sculpture

24 GOLDING ET AL.

\ N

й =

EEE ND

G<]

N
SEND

FIGS. 33-38. Anatomy of Dendropoma mejillonense Pacheco & Laudien, 2008. FIGS. 33, 34: Female specimen. Scale bars = 2 mm. FIG. 33: Right view of body; FIG. 34: Mantle cavity; FIG. 35: Leaflet from mid-section of gill. FMNH 312172, Peninsula Mejillones, Chile. Scale bar = 500 um; FIG. 36: Pallial vas deferens. Scale bar = 1 mm; FIG. 37: Pallial oviduct. Scale bar = 1 mm; FIG. 38. Unstalked egg capsules removed from mantle cavity of female. Scale bar = 1 mm. FIGS. 33, 34, 36-38: FMNH 312173, Peninsula Mejillones, Chile.

on teleoconch. The aperture is also raised
above the substratum by an extended section
of the shell (a feeding tube, but not developed
to the extent of some Petaloconchus species),
which is occasionally removed and extended, resulting in scars from abandoned feeding tubes. The protoconch is highly distinctive and sculptured with short gouges. Ceraesignum robinsoncrusoei n. sp. is also known from Chile, but occurs in another region and differs in shell, operculum, protoconch and animal morphology.

Taxonomic Remarks

The species epithet is here corrected to D. mejillonense to match the neuter generic name. A lectotype has been selected from among the syn-types deposited in the FMNH collections by the original authors (Pacheco & Laudien, 2008).

Distribution (Fig. 7)

Known only from the type locality at Peninsula Mejillones in northern Chile.

“DENDROPOMA GROUP” WORM-SNAILS 25

Dendropoma nebulosum
(Dillwyn, 1817)

“Tuyaux de mer” Davila, 1767: 562, pl. 4, fig. H [without locality].
“Rugose ridged worm” da Costa, 1770-1771: pl. 11, figs. 8-10 [West Indies; common name and locality from Jackson, 1937: 336]. “Vermiseaux intestins” d’Argenville, 1780: 652, pl. 6 fig. | [American Seas].
“Les Bourras tres-raboteux” d’Argenville, 1780: 667, pl. 6, fig: F2.
Serpula nebulosa Dillwyn, 1817: 1076-1077; Wood, 1828: 186, pl. 38, fig. 18; Bieler & Petit, 2011: 49.
Serpula bicarinata С. В. Sowerby ll, 1839: 116, fig. 4 [without locality].
Siphonium nebulosum — Mörch, 1859: 357-358 [St. Thomas]; Mörch, 1861: 162-163 (in part; Mörch listed eight infrasubspecific variet-ies, partly from specimens [Honduras, St. Thomas], partly based on earlier literature); Mörch, 1877: 112-114 [Honduras, St. Thom-as]; Clessin, 1902: 52-54; Jong & Coomans, 1988: 42-43, pl. 33, fig. 197 [Curacao, Aruba, Bonaire; unspecified].
Vermetus (Siphonium) nebulosus — Tryon, 1886: 184, 440, pl. 54, figs. 87, 88 [the latter fig. = Serpula bicarinata of С. В. Sowerby Il]. Dendropoma (Dendropoma) nebulosum — Keen, 1961: 199.
Spiroglyphus (Novastoa) nebulosus — Abbott, 1974: 101 [as nomen dubium].
Dendropoma nebulosum — Rawlings et al., 2001: 1604 [Florida Keys; sequence and gene arrangement data].
Serpulorbis riisei— Zhang, 2011: 69, fig. 126 [An-tigua; non Thylacodes riisei Mörch, 1862]. Dendropoma irregulare — Zhang, 2011: 69: fig. 128 [Antigua; non Vermetus irregularis d’Orbigny, 1841].

Type Locality

American Seas.

Material Examined

Specimens studied by Mörch (1861: 162-163), including his infrasubspecific forms “serrata” (NHMUK 1986.201; Honduras), “rugosa” and “fissurata” (NHMUK 1986.203), and “anaulax” (NHMUK 1986.199; Honduras).
Mexico (Yucatan): FMNH 286235 and 286237: Puerto Morelos, Quintana Roo, approx. 20.83°N, 86.88°W, coll. J. Templado, October 20, 1994, 70% EtOH (total 6 specimens).

Belize: FMNH 326923: patch reef, Carrie Bow Cay, Stann Creek District, 16.80°N, 88.08°W, coll. R. Bieler, March 22, 1986, 70% EtOH (4 adults with egg capsules) (many); FMNH 326934: patch reef, Carrie Bow Cay, Stann Creek District, 16.80°N, 88.08°W, coll. R. Bieler, March 1986, dry (6 specimens). Bahamas: FMNH 335070: 10-12 m, outside barrier reef off Walker’s Key, reefs NE of Great Abaco Island, 26.6410°N, 77.0374°W, coll. R. Bieler & P. Sierwald, August 8, 2012, 95% EtOH and dry [DNA sequence data]; FMNH 326963: Smiths Point, south shore, 4 km SE of Freeport, Grand Bahama Island, 26.5125°N, 078.6083°W, coll. J. Worsfold, January 9, 1989, 70% EtOH (many); FMNH 326964: 3-6 m, circular patch reefs with corals, gorgonians, sponges, known as “School House”, off Coral Harbour, SW New Providence Island, 24.97°N, 77.47°W, August 24, 1994, coll. R. Bieler & P. Sierwald, 70% EtOH (5 specimens).
Barbados: FMNH 326965: 18 m, coral reef, off Spring Garden, 13.116°N, 59.638°W, April 18, 1989, coll. P. M. Mikkelsen, 70% EtOH (many).
Florida, U.S.A.: FMNH 326966: 3m, from gorgo-nians, off Missouri Key, Florida Keys, Monroe County, 24.674°N, 81.238°W, October 15, 1988, R. Bieler & P. M. Mikkelsen, 70% EtOH (2 specimens); FMNH 290043: 5m, spur and groove reef, Looe Key, Lower Florida Keys, Monroe County, 24.5466°N, 81.4133°W, Au-gust 10, 1999, coll. R. Bieler & P. M. Mikkelsen, 70% EtOH (many); FMNH 315538, 327090: R/V Floridays, 7 m, “The Slabs” patch reef between outer patches and “coral humps” off Marathon, MM 50, Florida Keys, Monroe. County, 24.6588°N, 81.0150°W, July 20, 1997, coll. R. Bieler & P. M. Mikkelsen, 95% EtOH (many), [DNA sequence data]; FMNH 326734: small patch reef, off Newfound Harbor Keys, Monroe County, 24.6162°N, 81.3913°W, coll. R. Bieler & P. Sierwald, September 11, 2010, 70% EtOH (2 specimens), 3.5% glutaralde-hyde (1 sample of testis), RNAlater (2 tissue samples); FMNH 326736: ocean side of Ram-rod Key, Looe Key forereef, Monroe County, 24.5458°N, 81.4059°W, coll. R. Bieler & P. Sierwald, September 13, 2010, 80% EtOH (2 specimens), 3.5% glutaraldehyde (1 sample of testis), RNAlater (2 tissue samples).
Saba, Netherlands: FMNH 328794: 23 m, dive site “Hole in the Corner” off SE coast of Saba Island, 17.6167°N, 63.2283°W, coll. R. Bieler & P. Sierwald, October 15, 2010, 95% EtOH (5 specimens).

26 GOLDING ET AL.

Description

Teleoconch (Figs. 39-42): Size, shape and
sculpture highly variable between and within populations. Apertural diameter to 11.4 mm;
shell length to 30 mm; diameter of last whorl
to 28 mm. Up to four whorls, initial whorls coiled concentrically, sometimes shifting to off-center growth for later whorls; occasion-ally wrapped around cylindrical substratum (e.g. gorgonian stem); superficially attached to (if gorgonian) or shallowly entrenched in (if rock or shell) substratum; aperture usually flush with substratum, occasionally slightly raised; scars from abandoned feeding tubes absent. Exterior surface chalky white to cream or tan; sculpture of transverse lamellae crossed by 3-7 longitudinal ridges, central ridge dominant, transverse lamellae at apex of ridges forming spinose carinae. Interior surface cream on dorsal surface, dark brown on ventral surface.

Protoconch (Figs. 43-46): Hatchling proto-conch diameter to 670 um; height to 600 um. Sculpture absent on first 0.5 whorl, last 0.8 whorl with raised “crust” of cratered sculpture; spiral keel absent. Pale brown or colorless.

Operculum (Figs. 47-50): Diameter to 7.7 mm. Shallow conical; opaque dark orange to red around muscle attachment area, transparent golden peripherally, with ring of dark orange at margin. Lamina on exterior surface flat. Interior surface with moderately tall, conical mammilla.

Radula (Fig. 51): Length of ribbon 2.9 mm; up to 45 rows. Outer marginal tooth: one cusp on inner side.

External Morphology and Color (Figs. 52, 53, 55): Body length to 27 mm; occupying 1-2 whorls of shell. Columellar muscle extending for 0.5 whorl. Color in life: Head-foot black with white speckles, especially on snout, sides of head and sides of foot; cephalic and pedal tentacles black, with white speckles; mantle cream with dense, opaque, white pig-ment; mantle margin with alternating bands of black and white pigment; two morphs present, distinguished by either intense red or yellow pigment on sole of foot and diffuse red or yellow pigment overlaying entire foot and dorsal surface of head. Pigmentation of specimens preserved in 70% EtOH: head-foot cream to pale gray, dorsal surface of

head either mottled or entirely dark gray with dark patches on lateral surface of head at base of tentacles; cephalic tentacles pale gray; pedal tentacles dark gray.

Pallial and Reproductive Anatomy (Figs. 56-59): Gill with 22 leaflets per mm; leaflets medium-height, triangular, breadth equal to height. Osphradium short, 3.9 mm long; anterior tip curved towards columellar muscle. Rectum straight. Hypobranchial gland extending across rectum and proximal pallial oviduct. Pallial oviduct with notch at midpoint; proximal diverticulum present.

Development and Ecology (Figs. 54, 60): Up to eight unstalked egg capsules per female; 18-40 embryos per capsule. Late stages as pediveliger with small velar lobes, eye spots, shell suture and inner lip of aperture brown, and larval operculum with distinct orange spiral in center; head and foot in most cases pigmented with fine black spots. Adults solitary or gregarious, often found in association with living coral, gorgonians and Dendostrea frons.

Comparative Remarks

Similar to Novastoa pholetor, but without a mantle slit or ruffled lamina on operculum. The protoconch is typical covered by an irregular layer pitted with craters, which does not occur in any other Dendropoma species. The opercu-lum is distinct from other “concave-operculate” Dendropoma species because the mammilla is conical, not nipple shaped. The egg capsules of D. nebulosum contain 30-40 eggs, more than any other species of Dendropoma.

Taxonomic Remarks

Dillwyn (1817: 1076) introduced Serpula nebulosa based on a figure by Davila (1767: 562, pl. 4, fig. H) and text and figure by “Fa-vanne” [d’Argenville, 1780: 652, pl. 6, fig. |). D’Argenville (1780: 652), who considered the species American and uncommon, referred to Davila’s earlier illustration, and Mörch (1859: 357, 1861: 162) interpreted the later figure as a mere copy. Wood (1828: 186, pl. 38, fig. 18) pub-lished another, extremely sketchy, copy. Mörch (1859) transferred the species to Siphonium and in 1861 recognized it as highly variable and widely distributed in the Caribbean, prompting him to name eight infrasubspecific varieties. He (1859, 1861) synonymized Serpula bicarinata

“РЕМОКОРОМА GROUP” WORM-SNAILS 27

40

FIGS. 39-54. Dendropoma nebulosum (Dillwyn, 1817). FIG. 39: Living animal attached to coral at Carrie Bow Cay, Belize; FIG. 40: Shell with carinate sculpture. FMNH 326934, Carrie Bow Cay, Belize. Scale bar = 10 mm; FIG. 41: Shell without carinate sculpture. FMNH 286237, Yucatan, Mexico; FIG. 42: Specimens growing in clusters on gorgonian stems with Dendostrea frons. Scale bar = 10 mm; FIGS. 43-45: Proto-conchs removed from recently settled juveniles. FMNH 326963, Grand Bahama Island, Bahamas. Scale bar = 200 um. FIG. 43: Abapertural view; FIG. 44: Apertural view; FIG. 45: Apical view; FIG. 46: Sculpture on protoconch. Scale bar = 50 um; FIGS: 47-49: Operculum. FMNH 326963, Grand Bahama Island, Ba-hamas. Scale bar = 1 mm. FIG. 47: Exterior surface; FIG. 48: Lateral view; FIG. 49: Interior surface; FIG. 50: SEM image of exterior surface of operculum. FMNH 326963, Grand Bahama Island, Bahamas. Scale bar = 500 um; FIG. 51: Central section of radula. FMNH 326963, Grand Bahama Island, Bahamas. Scale bar = 50 um; FIGS. 52, 53: Living specimens from Carrie Bow Cay, Belize. FIG. 52: Red morph; FIG. 53: Yellow morph; FIG. 54: Two egg capsules removed from female specimen at Carrie Bow Cay, Belize.

28 GOLDING ET AL.

2

US x

FIGS. 55-60. Anatomy of Dendropoma nebulosum (Dillwyn, 1817). FIG. 55: Right view of male speci-men. FMNH 326963, Grand Bahama Island, Bahamas. Scale bar = 2 mm; FIG. 56: Mantle cavity of a male specimen. FMNH 326923, Carrie Bow Cay, Belize. Scale bar = 2 mm; FIG. 57: Leaflet from mid-section ofg ill. FMNH 326963, Grand Bahama Island, Bahamas. Scale bar = 200 um; FIG. 58: Pal-lial oviduct. FMNH 326923, Carrie Bow Cay, Belize. Scale bar = 2 mm; FIG. 59: Pallial vas deferens. FMNH 286235, Yucatan, Mexico. Scale bar =2 mm; FIG. 60: Unstalked egg capsules removed from the mantle cavity of a female, containing embryos at various stages of development. FMNH 326963, Grand Bahama Island, Bahamas. Scale bar = 1 mm.

С. В. Sowerby Il, 1839, from unknown locality,
and in 1877 Mörch recognized additional historic
illustrations, such as d’Argenville’s (1780: pl. 6,
fig. F2), as belonging to this nominal taxon. The
species was rarely mentioned in the subsequent literature, and Abbott (1974: 101) declared it an “undetermined species of dubious identity.” Various modern illustrations of this species can be found in the recent literature, misidentified as members of other species (e.g., Zhang, 2011, as “Serpulorbis riise? and “Dendropoma irregulare”). Dendropoma nebulosum is variable

within and between populations. In particular, the presence and prominence of carinose spines on the teleoconch is inconsistent. In at least one population (Carrie Bow Cay, Belize) distinct morphs with either red or yellow coloration on the head-foot were observed alive, but were not otherwise distinguishable.

Distribution (Fig. 7)

Common throughout the Caribbean, Baha-mas, and South Florida.

“DENDROPOMA GROUP” WORM-SNAILS 29

Dendropoma platypus
(Mörch, 1861)

Siphonium (Stoa) platypus Morch, 1861: 153, 157; Bieler & Petit, 2011: 53.
Siphonium platypus — Clessin, 1902: 48. Dendropoma (Dendropoma) platypus — Keen, 1961: 207.
Dendropoma platypus — Hadfield et al., 1972: 84-86, figs. 5, 6, 19H; Kay, 1979: 106, fig. 39B.

Type Locality

Sandwich [Hawaiian] Islands, оп a Chama; precise locality unknown.

Material Examined

Holotype: NHMUK 195927.
Hawaiian Islands, U.S.A.: FMNH 88577: Mokuoloe Island, Oahu, 157.7861°W, 21.4361°N, coll. T. Dranga, 1925, dry (3 specimens). FMNH 329359: beach rock on reef flats, 0.1 m at low tide, Diamond Head Beach, E Honolulu, Oahu, approx. 21.43°N, 157.79°W, coll. R. Bieler, March 28, 1988, 70% EtOH (2 specimens).
French Polynesia: UF 436992: channel wall with coral and silty slope with rubble, Teru-aupou Pass, Moorea Island, Society Islands; 17.5727°S, 149.7884°W, coll. G. Paulay, C. Meyer & S. McPherson, December 7, 2009, 75% EtOH (1 specimen).
Australia: AM C.464334: under beach rock slabs, just below beach, opposite laboratory, Heron Island, Capricorn Group, Queensland, 23.4434°S, 151.9126°E, coll. W. Е. Ponder, September 21, 1970, 5% SW formalin (2 specimens); AM C.407534: on semi-exposed boulder bank, Putta Putta Beach, S of Fly Point, Cape York Peninsula, Queensland, 10.7586°S, 142.5994°E, coll. W. F. Ponder & |. Loch, July 11, 1976, 5% SW formalin (many).

Description

Teleoconch (Figs. 61-64): Apertural diameter to 9 mm; shell length to 40 mm; diameter of last whorl to 21 mm. Up to four concentrically coiled whorls, last whorl sometimes straight-ening out; deeply entrenched in substratum; aperture flush with substratum; scars from abandoned feeding tubes absent. Exterior surface often heavily encrusted, but where exposed white, sometimes mottled brown,

purple or green (Hadfield et al., 1972); sculp-ture of low, thick, transverse lamellae crossed by many (> 10) longitudinal ribs, at apex of each rib transverse lamellae sometimes form carinae. Interior surface of shell white with ir-regular brown patches on ventral surface.

Protoconch (Figs. 65, 66): Settled protoconch diametert o 560 um; height to 610 um. Sculp-ture of shallow craters on first 0.6 whorl, last 0.7 whorl with tall, widely-spaced axial ribs; spiral keels absent. Pale brown.

Operculum (Figs. 67—72): Diameter to 5 mm. Shallow conical; either dark red around muscle attachment area and colorless periph-erally (living Hawaiian specimens, according to Hadfield et al., 1972, and preserved Putta Putta Beach specimens), or opaque orange around muscle attachment area and transpar-ent golden peripherally (preserved Hawaiian and Heron Island specimens). Lamina on exterior surface either flat or raised for ap-prox. one revolution. Interior surface with moderately tall, nipple-shaped mammilla.

Radula (Fig. 73): Length of ribbon 2.8 mm; up to 53 rows. Outer marginal tooth: two cusps on inner side.

External Morphology and Color (Figs. 74, 75): Body length to 35 mm; occupying last 1-2 whorls of shell. Columellar muscle extend-ing for one whorl. Color in life (modified from Hadfield et al., 1972): Head-foot black with yellow and white speckles especially on sides of head; mantle margin with alternating bands of black and bright yellow. Color of speci-mens preserved in 70% EtOH: Head-foot flesh-colored, dorsal surface of head gray; cephalic tentacles unpigmented with dark gray patches at base; mantle cream with pale grey pigment band behind margin.

Pallial and Reproductive Anatomy (Figs. 76— 79): Gill with 17 leaflets per mm; leaflets tall triangular, height twice breadth. Osphradium short-medium length, 5.3 mm long; anterior tip curved towards columellar muscle. Rec-tum straight. Hypobranchial gland extending partly across rectum. Pallial oviduct without notch at midpoint; proximal diverticulum present.

Development and Ecology: At least five un-stalked egg capsules per female; up to 70 larvae per capsule (Hadfield et al., 1972;

30 GOLDING ET AL.

based on Hawaiian material). Larval devel- capable of swimming (Hadfield et al., 1972),
opment mixed: laboratory-reared recently whereas veligers obtained by plankton tow re-
hatched larvae with resorbed velum, not ported by Taylor (1975: 77) were smaller and

61

FIGS. 61-73. Dendropoma platypus (Mörch, 1861). FIG. 61: Two specimens entrenched in substratum (apertures marked with asterisks) surrounded by Dendropoma gregarium. FMNH 329359, Oahu, Ha-waii. Scale bar = 10 mm; FIG. 62: Shell with dorsal keel. AM C.407534, Putta Putta Beach, Australia. Scale bar = 5 mm; FIG. 63: AM C.464334, Heron Island, Australia. FIG. 64: SEM image of teleoconch sculpture. AM C.464334, Heron Island, Australia. Scale bar = 500 um; FIGS. 65, 66: SEM images recently-settled protoconchs. FIG. 65: Apical view. AM C.407534, Putta Putta Beach, Australia. Scale bar = 100 um; FIG. 66: Abapertural view, partly obscured by later whorls. FMNH 88577, Oahu, Hawaii. Scale bar = 200 um; FIGS. 67-70: Operculum. Scale bar = 1 mm. FIG. 67: Exterior surface. FMNH 329359, Oahu, Hawaii; FIG. 68: Lateral view. FMNH 329359, Oahu, Hawaii; FIG. 69: Lateral view. AM C.464334, Heron Island, Australia; FIG. 70: Interior surface. FMNH 329359, Oahu, Hawaii; FIGS. 71, 72: SEM images of operculum. AM C.464334, Heron Island, Australia. Scale bar = 500 um. FIG. 71: Muscle attachment area on interior surface; FIG. 72: Exterior surface; FIG. 73: Central section of radula. FMNH 329359, Oahu, Hawaii. Scale bar = 50 um.

“DENDROPOMA GROUP” WORM-SNAILS 31

ag

FIGS. 74-79. Anatomy of Dendropoma platypus (Mörch, 1861). FIG. 74: Right view of male speci-men. FMNH 329359, Oahu, Hawaii. Scale bar = 5 mm; FIG. 75: Right view of anterior body of male specimen. Scale bar = 5 mm. AM C.407534, Putta Putta Beach, Australia; FIG. 76: Mantle cavity of male specimen. FMNH 329359, Oahu, Hawaii. Scale bar = 5 mm; FIG. 77: Leaflet from mid-section of gill. AM C.407534, Putta Putta Beach, Australia. Scale bar = 500 um; FIG. 78: Pallial vas deferens. ЕММН 329359, Oahu, Hawaii. Scale bar = 2 mm; FIG. 79: Pallial oviduct. AM C.464334, Heron Island, Australia. Scale bar =2 mm.

metamorphosed within hours of collecting.
Adults solitary. Healy (1988) studied material
originally collected at Fly Point, Somerset,
Cape York Peninsula, northern Queensland
for sperm (AM C.407534, vidi).

Comparative Remarks

Dendropoma platypus is the only “concave-operculate” Dendropoma species to have axial ribs on the protoconch, a character that is shared with some “convex-operculate” species of Dendropoma. The ribs are tall and widely spaced, unlike other species of “convex-opercu-

late” Dendropoma that have low, closely-packed axial ribs on the protoconch, often in combina-tion with spiral sculpture or spiral keels.

Taxonomic Remarks

Material from three different Pacific regions has been assigned here to D. platypus. The Hawaiian material most likely belongs to this nominal species as it was collected in the region of the (still broadly stated) type locality and is concordant with the original description. Material from Moorea (French Polynesia) and Australia (Heron Island, Great Barrier Reef and

32 _ GOLDING ET AL.

Putta Putta Beach, Cape York) show some mi-
nor differences in anatomy but have been tenta-
tively included in D. platypus in order to avoid the premature introduction of new names. This hy-
pothesis should be tested using molecular data
and, especially, observations ofthe color ofliving animals from these localities and others sites in the South Pacific Ocean. Differences between populations, relative to the Hawaiian material, include: a more deeply concave operculum from Moorea; deep red pigment around the muscle attachment area (Australia); and solid rather than broken pigment around the mantle margin (Heron Island, Putta Putta Beach). However, the protoconchs from at least two localities match those from Hawaii and the shells and animals are generally very similar.
Faucci (2007), in her sampling of cytochrome oxidase subunit 1 (COI) from 170 specimens of D. platypus from the Hawaiian archipelago and surrounding Pacific islands, uncovered three strongly supported clades of D. platypus sepa-rated by large genetic distances (clades A, B, and C in Faucci, 2007). Whether such genetic divergence warrants species level distinction awaits further comparison of the genetics, mor-phology, and life-history of these specimens. All three clades include specimens collected from the Hawaiian Islands, the broadly stated type locality for this species.

Distribution (Fig. 7)

Central and southern Pacific Ocean be-tween Hawaii, French Polynesia and norther Australia. E

. Dendropoma cf. petraeum
(Monterosato, 1884).
[species complex]

? Vermetus glomeratus Bivona-Bernardi, 1832: 7, pl. 2, fig. 5 [see Bivonia petraeal.
? Vermetus cristatus Biondi, 1859: 120, pl. fig. 8.
? Bivonia petraea Monterosato, 1884a: 81, 1884b: 61 [introduced as а nomen novum for Vermetus glomeratus Bivona-Bernardi, 1832 (p. 7, pl. 2, fig. 5) non Serpula glomerata Lin-naeus, 1758]; Bieler & Petit, 2011: 51.
? Spiroglyphus glomeratus — Clessin, 1912: 112, 113: р: 81190189571, 2:
? Dendropoma (Novastoa) petraeum Keen, 1961: 200.
? Dendropoma (Novastoa) cristatum (Biondi, 1857 [sic]) — Scuderi, 1995: 5.

Dendropoma petraeum — Calvo et al., 1998: 525 ff. (reproductive biology); Rawlings et al., 2001: 1604 ff. (sequence and gene arrange-ment data).
Dendropoma petraeum [Western clade] — Calvo et al., 2009: 903 ff. (sequence data, larval shell morphology).

Type Locality

Mare di Palermo, Sicily, Italy, Mediterranean Sea.

Material Examined

Spain: FMNH 286238: intertidal, Cabo de Gata, Almeria, 36.780°М, 2.245°W, coll. unknown, February 3, 1995, 70% EtOH (5 specimens); FMNH 327231: Cabo de Palos, Murcia, 37.633°N, 0.699°E, coll. J. Templado, March 29, 1999, 95% EtOH (10 specimens) [DNA sequence data]. This material corre-sponds with (and are vouchers for) the “CG” and CP” locales in the Calvo et al. (2009) publication. ce |

Description

Teleoconch (Figs. 80-82): Apertural diameter to 3.6 mm; shell length to 13 mm; diameter Of last whorl to 7.5 mm. Up to four whorls, initially coiled concentrically, later whorls off-center; shallowly entrenched in substratum; aperture flush with substratum; scars from abandoned feeding tubes absent. Exterior ‚surface bluish-gray; sculpture of low, trans-verse lamellae crossed by up to five weak longitudinal ribs on dorsal surface, transverse lamellae not forming carinae. Interior surface bluish-gray to dark brown.

Protoconch (Fig. 83): Settled protoconch diam-eter to 630 um, height not determined due to overgrowth of teleoconch. Sculpture absent; spiral keels absent. Pale brown.

Operculum (Figs. 84—88): Diameter to 2.6 mm. Flat to slightly domed (flattened “mushroom-shaped”); dark burgundy with transparent margins. Lamina on exterior surface stacked. Interior surface slightly concave, with very low, conical mammilla.

Radula (Fig. 89): Length of ribbon 1.9 mm; up to 40 rows. Outer marginal tooth: 2 cusps on inner side.

“DENDROPOMA GROUP” WORM-SNAILS 33

External Morphology and Color (Figs. 90, 91): Body slender, length to 37 mm; occupying three whorls of shell. Columellar muscle extending 0.5 whorl. Color of specimens preserved in 70% EtOH: head-foot pale gray, dorsal surface of head with diffuse triangular patch of dark gray pigment behind snout and single stripe of black pigment crossing each cheek, outer surface of tentacle and side of

pallial oviduct. Pallial oviduct without notch at midpoint; proximal diverticulum present.

Development and Ecology: Egg capsules not found in examined material. Calvo et al. (1998) reported that D. petraeum from south-ern Spain produced up to 86 unstalked egg capsules containing one (occasionally two)
embryos per capsule. Adults reef-building.
snout; cephalic tentacles otherwise unpig-
mented; mantle cream with narrow band of Comparative Remarks
black pigment.
Shell is bluish-gray, unlike other species
Pallial and Reproductive Anatomy (Figs. 92-94): of Dendropoma. The operculum superficially Gill with 18 leaflets per mm. Osphradium short, resembles that of the “convex-operculate” 1.1 mm long; anteriotri p curved towards colu- Dendropoma species, but the “mushroom-mellar muscle. Rectum straight. Hypobranchial shape” is lost and the operculum is almost flat. gland extending across rectum and proximal The stacked layers of the spiral lamina on the

FIGS. 80-89. Dendropoma cf. petraeum (Monterosato, 1884). FMNH 286238, Cabo de Gata, Spain. FIG. 80: Cluster of specimens removed from substratum. Scale bar = 5 mm; FIG. 81: Adult shell. Scale bar = 2 mm; FIG. 82: SEM image of teleoconch sculpture. Scale bar = 200 um; FIG. 83: Protoconch removed from adult shell. Scale bar = 100 um; FIGS. 84-88: Operculum. Scale bars = 500 um. FIG. 84: Exterior surface; FIG. 85: Lateral view; FIG. 86: Interior surface; FIG. 87: SEM image of exterior surface; FIG. 88: SEM image of interior surface; FIG. 89: Central section of radula. Scale bar = 50 um.

34 GOLDING ET AL.

(9)A S

Be

:7IRE

ANG
С
RM

Sr)

2

Qc&

U

e

FIGS. 90-94. Anatomy of Dendropoma cf. petraeum (Monterosato, 1884). FMNH 286238, Cabo de Gata, Spain. FIG. 90: Right view of female specimen. Scale bar = 2 mm; FIG. 91: Dorsal view of head of female specimens. Scale bar = 1 mm; FIG. 92: Anatomy of mantle cavity of a male specimen. Scale bar = 2 mm; FIG. 93: Pallial oviduct. Scale bar = 1 mm; FIG. 94: Pallial vas deferens. Scale bar = 1 mm.

exterior surface are greatly reduced, and the
conical mammilla on the interior surface is very
low. The presence of multiple longitudinal ribs
on the teleoconch, without carinose spines, is
also unique in Dendropoma.

Taxonomic Remarks

The species identity of Dendropoma cf. petraeum is uncertain due to a recent mo-lecular analysis that found significant genetic separation between four Mediterranean regions indicative of a cryptic species complex (Calvo et al., 2009). The material used in this study is from southeast Spain, falling within the “western clade” of their analysis, specifically

their CG and CP sample groups, which the authors found distinct from a Central clade sampled from Sicily, Malta, and the Tyrrhenian Sea (Corsica and Western Italy). Protoconch morphology varies between “molecular clades”, and the protoconchs of the material examined here were smooth, supporting its position in the “western clade.” Calvo et al. (2009) de-scribed developmental characters separating the clades (egg capsule number, number of eggs per capsule), but few adult-morphological differences. Dendropoma cristatum (Biondi, 1859) was recognized as an available senior synonym of D. petraeum (Monterosato, 1884) by Scuderi (1995). The type material of both Vermetus glomeratus (= Bivonia petraea) and

“DENDROPOMA GROUP” WORM-SNAILS 35

V. cristatus stems from the Central clade re-gion, suggesting a link between these names and that clade, but further investigation of the original material (and, potentially, re-sampling of the exact type localities) will be necessary to properly connect the available names to the clades recognized by molecular studies.

Distribution (Fig. 7)

Examined material from southeast Spain, but see Taxonomic Remarks.

Dendropoma cf. corrodens
(d’Orbigny, 1841)

Vermetus corrodens d’Orbigny, 1841: 235-236, pl. 18, figs. 1-3 (Cuba and Martinique); Gray, 1854: 14; Clessin, 1912: 116, pl. 15, figs. 1, 3, 4 [after d'Orbigny]; Bieler & Petit, 2011: 32. Spiroglyphus corrodens — Mörch, 1860: 44. Spiroglyphus annulatus Daudin, 1800, Mörch, 1860: 44; 1862: 330-331; 1877: 114-116; Clessin, 1912: 108, 109; Morrison, 1968: 45-46; Abbott, 1974: 100; Rehder, 1981: 429, fig. 100 [name placed on the Official Index of Rejected and Invalid Specific Names in Zool-ogy by Opinion 1425 (1.C.Z.N. 1987)]. Spiroglyphus annulatus var. a “dentifera” of Mörch, 1862: 331 [an infrasubspecific name introduced for d’Orbigny’s V. corrodens)]. Spiroglyphus annulatus var. 6 “trochicola” of Mörch, 1862: 332 [an infrasubspecific name introduced for material from St. Thomas]. Vermetus (Spiroglyphus) annulatus var. cor-rodens — Tryon, 1886: 178, 438, pl. 51, fig. 51 [after d’Orbigny, 1841].
Dendropoma (Dendropoma) corrodens — Keen, 1961: 199, 206.
Dendropoma (Novastoa) irregulare — Morton, 1965: 588 ff., fig. 4 [gross anatomy, oper-culum; Jamaica; non Vermetus irregularis d’Orbigny, 1841].
Dendropoma corrodens — Rawlings et al., 2001: 1604 ff. [sequence and gene arrange-ment data].

Type Locality

Cuba and Martinique, precise locality un-known.

Material Examined

Syntypes: NHMUK 54.10.4.159. Original mate-rial studied by Mórch (1862: 330-332), includ-ing his var. В (NHMUK 1986.205).

Florida, U.S.A.: FMNH 327050: Missouri Key, Florida Keys, 24.674°N, 81.238°W, coll. К. Bieler, September 1989, dry (many); FMNH 326955: shallow-water beach with old coral/ beach rock, partly exposed at low tide, Mis-souri Key, Florida Keys, 24.674°N, 81.238°W, coll. R. Bieler & P. Sierwald, June 10, 1985, 70% EtOH (many); FMNH 326960: shallow-water beach with old coral/beach rock, partly exposed at low tide, Missouri Key, Florida Keys, 24.674°N, 81.238°W, coll. К. Bieler 8 P. M. Mikkelsen, April 10, 1988, 70% EtOH (many); FMNH 293171: exposed beach rock at low tide and dead gorgonians on beach, Atlantic side of Missouri Key, Florida Keys, 24.6747°N, 81.2392°W, coll. К. Bieler € P. M. Mikkelsen, January 15, 1994, 70% EtOH (many) [DNA sequence data]; FMNH 306129: collected by hand from intertidal rocks at low tide, oceanside Missouri Key, Florida Keys, 24.674°N, 81.238°W, coll. R. Bieler 8 P. M. Mikkelsen, April 29, 2004, 70% EtOH (many); FMNH 326592: oceanside of Missouri-Ohio Key bridge, Missouri Key, Monroe County, U.S.A., 24.6747°N, 81.2392°W, coll. R. Bieler & P. Sierwald, April 28, 2010, 70% EtOH (many), 3.5% glutaraldehyde (many), 95% EtOH (many), formalin (many) and dry (many).
Bahamas: FMNH 326947: intertidal, Silver Point, Grand Bahama Island, 26.50°N, 78.66°W, coll. J. Worsfold, January 8, 1989, 70% EtOH (many); FMNH 326962: rocks, sand and algae at 2 m depth, near Chub Cay, off Whale Cay, 25.41°N, 77.84°W, coll. P. M. Mikkelsen, October 17, 1987, 70% EtOH (many).
Turks and Caicos Islands: W coast of Salt Cay, - 21°19.65’N, 71°12.94’W, coll. К. Bieler 4 P. Sierwald, April 16, 2004, 70 EtOH (many). Cayman Islands: FMNH 328947 and 328948: intertidal rocky shore at Spotts Beach, Grand Cayman, 19.2724°N, 81.3159°W, coll. L. Dombowsky, January 11-13, 2011, 70% EtOH (many); FMNH 328949: intertidal rocky shore at East End, Grand Cayman, 19.2934°N, 81.1194°W, coll. L. Dombowsky, January 13, 2011, 70% EtOH (many).
U.S. Virgin Islands: FMNH 326944: Tague Bay, St Croix, 17.757°N, 64.612°W, coll. M. Had-field & R. Bieler, March 3, 1987, 70% EtOH (many); FMNH 327001: 10-15 m depth, Long Reef, S of Christiansted, St. Croix, coll. R. Bieler & N. Ogden, February 28, 1987, 70% EtOH (many); FMNH 326968: Columbus Landing, St. Croix, 17.779°N, 64.759°W, coll. R. Bieler, March 2, 1987, 70% EtOH (many);

36 GOLDING ET AL.

FMNH 326969: reef off Tague Bay, St. Croix,
approx. 17.7°М, 64.6°W, coll. M. С. Hadfield,
February 28, 1987, 70% EtOH (many);
FMNH 327241: Boiler Bay, E of West Indies
Laboratory (WIL) of the Fairleigh Dickinson
University, St. Croix, 17.7625°N, 64.5786°W, coll. R. Bieler, March 3, 1937.
Guana Island, British Virgin Islands: FMNH 326699: 2-3 m, patch reefs, White Bay, 18.4708°М, 64.5739°W, coll. К. Biele&rТ . M. Collins, August 5, 2010, 70% EtOH (many) [DNA sequence data]; FMNH 326712: 5-6 m, near Monkey Point, White Bay, 18.4662°N, 64.5716°W, coll. В. Bieler & Т. M. Collins, August 8, 2010, 70% EtOH (10) [DNA se-quence data]; FMNH 326709; exposed spit on SW side of bay, across from Pirate’s Bight, Normal Island Bay, 18.4788°N, 64.6094°W, coll. R. Bieler & T.M. Collins, August 7, 2010, dry, 70% EtOH (10); FMNH 326718: 5-9 m, Guana Cove, at Iguana Head, 18.4745°N, 64.5823°W, coll. R. Bieler & T. M. Collins, August 9, 2010, 70% EtOH (10). | Saba, Netherlands: FMNH 328792: dive site “Hole in the Corner”, near shore, off SE coast of Saba Island, 17.616672°N, 63.226369°W, coll. R. Bieler & P. Sierwald, October 15, 2010, 95% EtOH (many).
Dominica: FMNH 335863, NE coast, St. An-drew Parish, Calibishi Beach, 15.5932°N, 61.3503°W, coll. R. Bieler & P. Sierwald, August 1978, on Fissurella nodosa (Born, 1778), many.
St. Lucia: FMNH 335795, NW end of island, Gros Islet Bay, 14.0868°N, 60.9561°W, coll. R. Bieler & P. Sierwald, August 1978, on Va-sum capitellum (Linnaeus, 1758), many. Barbados: FMNH 326960: coral reef, 18 m, off Spring Gardens, 13.12°N, 59.638°W, coll. P. M. Mikkelsen, April 18, 1989, 70% EtOH (many); FMNH 327095: limestone rocks and base of cliffs at mouth of estuary, River Bay, 13.3232°N, 59.5958°W, coll. R. Golding, T. Rawlings & C. McVarish, August 10, 2010, 10% SW formalin (many), [DNA sequence data]. FMNH 327096: fringing reef, Six Mens Bay, West coast, 13.2682°N, 59.6451°W, coll. R. Golding, T. Rawlings & C. McVarish, August 11, 2010, 100% EtOH, 10% formalin, [DNA sequence data].
Belize: FMNH 327009: Carrie Bow Cay, Stann Creek District, 16.803°N, 88.082°W, coll. R. Bieler, March 1986, 70% EtOH (many); FMNH 327142: on coral rubble, 2 m, SW from boat launch, Carrie Bow Cay, Stann

Creek District, 16.8021°N, 88.0825°W, coll. R. Bieler, R. Golding, T. Rawlings, T. Collins & P. Sierwald, April 14, 2011, dry, 70% EtOH, RNAlater, 95% EtOH (many) [DNA sequence data]; FMNH 327155: on coral boulders on reef сгез 0-1 m, Columbus Reef, Carrie Bow Cay, Stann Creek District, 16.9031°N, 88.0602°W, coll. R. Bieler, R. Golding, T. Rawlings, T. Collins & P. Sierwald, April 18, 2011, dry, 70% EtOH, RNAlater, 95% EtOH, 10% formalin (many).
Venezuela: FMNH 326967: off Quinzandal Beach (INTECMAR station), Puerto Cabello, Carabobo, 10.4747°N, 68.0203°W, coll. R. Bieler & P. Miloslavich, June 1, 1986, 70% EtOH (many).

Description

Teleoconch (Figs. 95-98): Apertural diameter to 1.8 mm; shell length to 10 mm; diameter of last whorl 6 mm. Up to four whorls, coiled concentrically initially, but later whorls tend-ing to straighten; either deeply entrenched in substratum or rising vertically in aggre-gate matrix; aperture flush with substratum; scars from abandoned feeding tubes absent. Exterior surface dark purplish-brown in life, fading to medium brown; sculpture of tall, closely-packed, vertical, transverse lamellae, “pinched together’ to form weak crest on dor-sal surface. Interior surface dark brown.

Protoconch (Figs. 99-102): Settled protoconch diameter to 430 um, height to 450 um. Sculp-ture absent on first 0.7 whorl, last 0.6 whorl with low, closely- or widely-spaced axial ribs (varying between populations); three weak spiral keels usually present. Honey brown.

Operculum (Figs. 103-111): Diameter to 1.5 mm. Highly variable in shape between and within populations. Domed, “mushroom-shaped”; dark burgundy with transparent margins. Lamina on exterior surface stacked. Interior surface concave, with low, conical mammilla.

Radula (Fig. 112): Length of ribbon 1.3 mm; up to 35 rows. Outer marginal tooth: two cusps on inner side.

External Morphology and Color (Figs. 95, 113, 114): Body slender, length to 20 mm; occupy-ing 2-3 whorls of shell. Columellar muscle extending 1 whorl. Color in life: Head-foot

“DENDROPOMA GROUP” WORM-SNAILS of

FIGS. 95-112. Dendropoma cf. corrodens (d’Orbigny, 1841). FIG. 95: Living specimen with pedal tentacles emerging from aperture. FMNH 326592, Florida Keys, U.S.A. Scale bar = 1 mm; FIG. 96, 97: Adult shells. Scale bars = 2 mm. FIG. 96: FMNH 326955, Florida Keys, U.S.A.; FIG. 97: FMNH 326962, Whale Cay, Bahamas; FIG. 98: SEM image of teleoconch sculpture. FMNH 327050, Florida Keys, U.S.A. Scale bar = 200 um; FIGS. 99-102: SEM images of protoconchs removed from recently settled juveniles from different areas of the Caribbean, apical views. Scale bar = 100 um. FIG. 99: FMNH 326955, Missouri Key, Florida; FIG. 100: FMNH 326968, St Croix, US Virgin Islands; FIG. 101: FMNH 326699, Guana, British Virgin Islands; FIG. 102: FMNH 328949, Grand Cayman, Cayman Islands; FIGS. 103-105: Operculum. FMNH 326955, Missouri Key, Florida. Scale bar = 500 um. FIG. 103: Exterior surface; FIG. 104: Lateral view; FIG. 105: Interior surface; FIGS. 106-110: SEM images of opercula from different areas of the Caribbean, lateral views. Scale bar = 100 um. FIG. 106: FMNH 293171, Missouri Keys, Florida; FIG. 107: FMNH 328949, Grand Cayman, Cayman Islands; FIG. 108: FMNH 326968, St Croix, US Virgin Islands; FIG. 109: FMNH 326962, Whale Cay, Bahamas; FIG. 110: FMNH 327009, Carrie Bow Cay, Belize; FIG. 111: SEM image of muscle attachment area on interior surface of operculum. FMNH 327050, Florida Keys, U.S.A. Scale bar = 100 um; FIG. 112: Central section of radula. FMNH 306129, Florida Keys, U.S.A. Scale bar = 50 um.

38 GOLDING ET AL.

ct

FIGS. 113-118. Anatomy of Dendropoma cf. corrodens (d’Orbigny, 1841). Scale bars = 1 mm. FIG. 113: Left view of female specimen; FIG. 114: Right view of anterior body. FMNH 326960, Florida Keys, U.S.A.; FIG. 115: Mantle cavity of male specimen; FIG. 116: Pallial oviduct; FIG. 117: Pallial vas defer-ens; FIG. 118: Unstalked egg capsule removed from female mantle cavity. FIGS. 113, 115-118: FMNH 326592, Florida Keys, U.S.A.

white with mottled black pigment anteriorly; Pallial and Reproductive Anatomy (Figs. 115- dorsal surface of head with diffuse bright yel-
low pigment and scattered superficial white
speckles, increasing in density around base
of tentacles, snout and sides of foot; sole of
foot white to rose pink; pedal tentacles trans-
parent with white speckles; cephalic tentacles white with black band at base, surrounded by white pigment patches on surface of head. Color of specimens preserved in 70% EtOH: head-foot mottled grey and white; cephalic tentacles white with black pigment at base; mantle cream.

117): Gill with 20 leaflets per mm. Osphradium short, 1.3 mm long; anteriotri p curved towards columellar muscle. Rectum straight. Hypo-branchial gland not extending across rectum. Pallial oviduct without notch at midpoint or proximal diverticulum.

Development and Ecology (Fig. 118): Up to five unstalked egg capsules per female observed herein (up to eight according to Miloslavich & Penchaszadeh, 1992); 4-9 embryos per capsule. Adults reef-building.

“DENDROPOMA GROUP” WORM-SNAILS 39

Comparative Remarks

Belonging to the “convex-operculate” group of Dendropoma - D. cf. corrodens, D. gregarium, D. howense, D. cf. tholia, D. psarocephalum and D. expolitum п. sp. — that share very similar shell and operculum morphology and similar coloration of the animals (where known). The protoconch of D. cf. corrodens has closely-spaced axial ribs, like D. howense, D. gregarium and D. cf. tholia, but lacks the spiral sculpture of D. gregarium and D. cf. tholia. Dendropoma cf. corrodens has a purplish-brown shell with prominent, upright transverse lamellae, unlike the pinkish-white shell with relatively smooth transverse lamellae of D. howense.

Taxonomic Remarks

The original type localities (given by d’Orbigny as Cuba and Martinique) were not sampled in this study, so we cannot definitely refer the examined material to D. corrodens. At the pres-ent state of knowledge, we are considering this species to have a pan-Caribbean distribution. However, because of ongoing research in this complex pointing to regional morphological dif-ferences (in density and height of axial ribs on the protoconch) and high levels of mtDNA diver-gence among samples collected to date (up to 18% (uncorr.-P), we are using the tentative name D. cf. corrodens for our studied material. Mörch (e.g., 1862: 330-332) considered V. corrodens and Vermetus irregularis d’Orbigny, 1841, to be members of a single species. The type material of the latter species (also de-scribed from Cuba and Martinique; syntypes in MNHUK, vidi) does not seem to be сопзре-cific, and even its generic position is presently unresolved.
The name Spiroglyphus annulatus Daudin, 1800, was in wide use for this gastropod taxon until it was placed on the Official Index of Re-jected and Invalid Specific Names in Zoology by Opinion 1425 (1.C.Z.N., 1987). However, various malacological works figured polychaete worms under this name (e.g., Vokes & Vokes, 1983: pl. 4, fig. 16, as S. annulatus; Daccarrett & Bossio, 2011: 245, fig. 358, as "Dendropoma annulatus”). The confusion with serpulid worms continues under its present name, Dendropoma corrodens (e.g., Tunnell et al., 2010: 136).

Distribution (Fig. 7)

Common throughout the Caribbean, Baha-mas, and South Florida.

Dendropoma gregarium
Hadfield & Kay, 1972

Dendropoma gregaria [sic] Hadfield & Kay in Hadfield, Kay, Gillette & Lloyd, 1972: 81-83, figs. 1-2, 19A; Kay, 1979: 103, 104, fig. 38. Dendropoma gregarium — Rawlings et al., 2001: 1604 [sequence and gene arrangement data]; Bieler & Petit, 2011: 40.

Type Locality

On intertidal boulders, Kaheka (near Koloa), Kauai, Hawaii: 21.8750°N, 159.6416°W.

Material Examined

Holotype and paratypes: BPBM 8929. Hawaiian Islands, U.S.A.: FMNH 326970: Oahu, approx. 21.3°М, 157.9°W, cell. В. Bieler, March 1988, 70% EtOH (many); FMNH 326971: shallow water, old reef flat, Kaneohe Bay, Oahu, 21.45°N, 157.79°W, coll. R. Bieler, December 1986, 70% EtOH (many); FMNH 326972: 0.1 m at low tide, beach rock on reef flats, Diamond Head Beach, Oahu, approx. 21.43°N, 157.79°W, coll. R. Bieler, March 28, 1983, 70% EtOH (many); FMNH 318222: Oahu, coll. M. Had-field, 70% EtOH (6) [DNA sequence data]; AM C.407557: exposed rocky platform, Diamond Head, Oahu; 21.267°N, 157.817°W., coll. W. Е. Ponder & Е.А. Kay, April 6, 1974, 10% SW formalin (many).

Description

Teleoconch (Figs. 119, 120): Apertural diameter to 3 mm; shell length to 12 mm; diameter of last whorl to 7 mm. Up to four whorls, coiled concentrically initially, but later whorls tend-ing to straighten; either deeply entrenched in substratum or rising vertically in aggregate matrix; aperture flush with substratum; scars from abandoned feeding tubes absent. Exte-rior surface deep purplish-black in life (Had-field et al., 1972), fading to medium brown; sculpture of tall, closely-packed, transverse lamellae, without a longitudinal crest or ridges. Interior surface dark brown.

Protoconch (Figs. 121-123): Hatchling proto-conch diameter to 450 um, height to 360 um (900 um by 650 um according to Hadfield et al., 1972). Sculpture absent on first 0.6 whorl, last 0.7 whorl with very weak axial ribs crossed by broken, spiral threads breaking

40

into pustules near lip; spiral keels absent. Pale brown.

Operculum (Figs. 124-128): Diameter to 2.0 mm. Domed, “mushroom-shaped”; dark burgundy with transparent margins. Lamina on exterior surface stacked. Interior surface concave, with low, conical mammilla.

GOLDING ETAL.

whorls of shell. Columellar muscle extend-ing one whorl. Color in life (modified from Hadfield et al., 1972): Head-foot black with white speckles, especially on sides of head, snout gray; sole of foot either bright pink or light yellow without intergrades; cephalic tentacles black at base, white at tips; pedal tentacles transparent; mantle black except for white speckles on margin. Color of specimens preserved in 70% EtOH: colorless except for pale grey pigment on snout and black pig-ment at base of tentacles.

Radula (Fig. 129): Length of ribbon 1.0 mm; up to 32 rows. Outer marginal tooth: 2-3 cusps on inner side.

External Morphology and Color (Fig. 130): Body
slender, length to 20 mm; occupying 2-3

Pallial and Reproductive Anatomy (Figs. 131,
132): Gill with 17 leaflets per mm. Osphra-

129%

FIGS. 119-129. Dendropoma gregarium Hadfield & Kay, 1972. FIG. 119: A cluster of specimens re-moved from the substratum. Scale bar = 10 mm; FIG. 120: Adult specimen. Scale bar = 2 mm; FIGS. 121-123: SEM images of intracapsular larval shells. Scale bar = 100 um. FIG. 121: Apertural view; FIG. 122: Abapertural view; FIG. 123: Apical view; FIGS. 124-126: SEM images of opercula. Scale bar = 200 um. FIGS. 124, 125: Lateral views; FIG. 126: Oblique view of interior surface; FIGS. 127, 128: Operculum. FMNH 407557, Oahu, Hawaii. Scale bar = 200 um. FIG. 127: Exterior surface; FIG. 128: Interior surface; FIG. 129: Central section of radula. Scale bar = 20 um. FIGS. 119-126, 129: FMNH 326972, Oahu, Hawaii.

“DENDROPOMA GROUP” WORM-SNAILS 41

FIGS. 130-132. Anatomy of Dendropoma gregarium Hadfield & Kay, 1972. FIG. 130: Left view of female specimen. FMNH 326927, Oahu, Hawaii. Scale bar = 1 mm; FIG. 131: Mantle cavity of male specimen. AM C.4075557, Oahu, Hawaii. Scale bar = 1 mm; FIG. 132: Pallial oviduct. AM 0.407557, Oahu, Hawaii. Scale bar = 500 um.

dium short, 1.5 mm long; anterior tip curved
towards columellar muscle. Rectum straight.
Hypobranchial gland not extending across
rectum. Pallial oviduct without notch at mid-
point or proximal diverticulum.

Development and Ecology: 3-4 unstalked egg capsules per female; 6-21 embryos per capsule observed herein; Hadfield et al. (1972) recorded direct development with recently hatched larvae crawling. Adults reef-building.

Comparative Remarks

Belonging to the “convex-operculate” group of Dendropoma. The protoconch of D. gregar-ium has characteristic spiral bands of broken threads crossing weak axial ribs.

Faucci (2007) discovered extremely high levels of genetic variation in CO/ sequences among 248 individuals sampled within the Hawaiian Islands and across the Pacific. Many monophyletic groupings of haplotypes were island-specific or restricted to taxa sampled from closely positioned islands, reflecting the lower potential for planktonic dispersal in this direct-developing, albeit geographically wide-spread, species (Hadfield et al., 1972; Faucci, 2007). The nucleotide sequence of СО! from the specimen of D. gregarium sequenced in our study from Kaneohe Bay, Oahu (FMNH 318222), was most similar to haplotype 69 in Faucci’s (2007) phylogenetic analysis (match of 526 bp over a total length of 530 bp). This haplotype was nested within one of several ge-netically distinct clades of specimens sampled from Oahu.

42 GOLDING ET AL.

Distribution

Based on collections by Faucci (2007), D.
gregarium is common throughout the Hawaiian
Islands and Micronesia.

Dendropoma howense
(Iredale, 1937)

Veristoa howensis lredale, 1937: 254, pl. 17, fig. 8; Keen, 1961: 192; Bieler & Petit, 2011: 40.

Type Locality

Middleton Reef, Tasman Sea, Australia: 295°S s, 159.2"E l

Material Examined

Syntypes: AM C.060226: from type locality as above, coll. G. P. Whitley, April 1936, dry (many).
Australia: AM C.407559: pools, MTL, Signal Point, Lord Howe Island, New South Wales; 31.525°S, 159.065°E, coll. W. F. Ponder& P. H. Colman, April 21, 1978, 10% SW formalin (many); AM C.407572: on calcarenite rocks, E of cemetery, Point Hunter Reserve, Nor-folk Island, 29.067°S, 167.967°E, coll. W. F. Ponder & Е. К. Yoo, June 22, 1979, 10% SW formalin (many); AM C.407546: rubble bank and sand flats, Elizabeth Reef, Tasman Sea, 29.923°S, 159.045°E, coll. I. Loch, Decem-ber 10, 1987, 10% SW formalin (many); AM C.302896, SW of Rat Island, Houtman Abrol-hos, Western Australia, 28.72°S, 113.78°E, coll. S. White & C. White, March 1970, 10% SW formalin (many).

Description

Teleoconch (Figs. 133-136): Apertural diam-eter to 3 mm; shell length to 16 mm; diameter of last whorl to 10 mm. Up to four whorls, coiled concentrically initially, but later whorls tending to straighten; deeply entrenched in substratum; aperture flush with substratum; scars from abandoned feeding tubes absent. Exterior surface medium brown to pinkish-white; sculpture of low, closely-packed transverse lamellae initially upright, flattened in later whorls, without longitudinal crest or ridges. Interior surface medium brown.

Protoconch (Figs. 137-139): Settled proto-conch diameter to 480 um, height to 480

um. Sculpture absent on first 0.8 whorl, last 0.5 whorl with low, closely-spaced axial ribs; three very weak spiral keels present. Pale brown.

Operculum (Figs. 140-144): Diameter to 1.5 mm. Domed, “mushroom-shaped”; dark burgundy with transparent margins. Lamina on exterior surface stacked. Interior surface concave, with low, conical mammilla.

Radula (Fig. 145): Length of ribbon 1.2 mm; up to 34 rows. Outer marginal tooth: 1 cusp on inner side.

External Morphology and Color. Not known.

Pallial and Reproductive Anatomy: Not known.

Development and Ecology: Developmental biology not known. Adults reef-building.

Comparative Remarks

Belonging to the “convex-operculate” group of Dendropoma. The protoconch of D. howense is very similar to that of D. corrodens, but the adult shells differ in that D. howense is very pale and has flattened transverse lamellae. The distribution overlaps with D. expolitum n. sp., but the protoconch of the latter species is unsculptured and the shell is brown with very coarse transverse lamellae.

Taxonomic Remarks

The type locality of D. howense is Lord Howe Island, but material collected from various locations around Australia, including Norfolk Island, Elizabeth Reef and Rat Island (West-ern Australia) are morphologically similar and are here referred to D. howense. Protoconch sculpture is consistent between all examined populations.
Dendropoma howense is the type species of Veristoa Iredale, 1937, here confirmed as a ju-пог subjective synonym of Dendropoma s.s.

Distribution (Fig. 7)

Tasman Sea from the central Great Barrier Reef (southern extent not known), including Lord Howe and Norfolk Islands, and Rat Island, Houtman Abrolhos, Western Australia. It is not clear whether the distribution is continuous across northern or southern Australia.

“DENDROPOMA GROUP” WORM-SNAILS 43

133;

143

FIGS. 133-145. Dendropoma howense (Iredale, 1937). FIG. 133: A cluster of specimens attached to rock substratum. AM C.407559, Lord Howe Island, Australia. Scale bar = 5 mm; FIG. 134: Adult shell. Syntype AM C.060226, Middleton Reef, Tasman Sea, Australia. Sale bar = 1 mm; FIGS. 135, 136: Adult specimens with epifauna and algae partly removed. Scale bars = 2 mm. FIG. 135: AM C.407559, Lord Howe Island, Australia; FIG. 136: AM C.302896, Rat Island, Houtman Abrolhos, Australia; FIGS. 137-139: SEM images of protoconchs removed from recently settled juveniles. Scale bar = 100 um. FIG. 137: Apical view. AM C.407546, Elizabeth Reef, Tasman Sea, Australia; FIG. 138: Abapertural view. AM C.407572, Norfolk Island, Australia; FIG. 139: Apical view. AM C.302896, Rat Island, Houtman Abrolhos, Australia; FIGS. 140-143: Opercula. Scale bar = 200 um. FIG. 140: Exterior surface. AM C.407559, Lord Howe Island, Australia; FIG. 141: SEM image of lateral view of operculum. AM C.407559, Lord Howe Island, Australia; FIG. 142: SEM image of lateral view of operculum. AM C.407546, Elizabeth Reef, Tasman Sea, Australia; FIG. 143: Interior surface of operculum. AM C.407559, Lord Howe Island, Australia; FIG. 144: SEM image of muscle attachment area on interior surface of operculum. AM C.407546, Elizabeth Reef, Tasman Sea, Australia. Scale bar = 100 um; FIG. 145: Central section of radula. AM C.407559, Lord Howe Island, Australia. Scale bar = 50 um.

Dendropoma cf. tholia ? Vermetus (Dendropoma) tholia — Barnard,
Keen & Morton, 1960 1963: 148.

? Dendropoma tholia Keen & Morton, 1960: Type Locality
41, pl. 3, text-figs. 6-13, 20-22, 33; Morton,
1965: 588 ff. Inhaca Island, off Lorenco Marques, Mozam-bique.

Ad, GOLDING ET AL.

Material Examined remainder of shell entirely encrusted with
coralline algae, but shell length at least 6
Kenya: FMNH 328086: mid-littoral rock mm, diameter of last whorl at least 4.5 mm.
bench, Kimondo Reef, Diani Beach, 4.36°S, Unknown number of whorls coiled concen-
39.57°E, J.D. Taylor, October 2, 1977, dry trically, rising vertically through aggregate
(many). matrix; aperture flush with substratum; scars
from abandoned feeding tubes not visible.
Description Exterior surface pale brown when cleaned;
sculpture of low, transverse lamellae, without
Teleoconch (Figs. 146-148): Apertural di- longitudinal crest or ridges (Keen & Morton,
ameter to 2.0 mm (Keen & Morton, 1960); 1960). Interior surface dark brown.

FIGS. 146-156. Dendropoma cf. tholia Keen & Morton, 1960. FMNH 328086, Kimona, Kenya. FIG. 146: Encrusting layer of coralline algae and D. cf. tholia removed from substratum, with only apertures visible. Scale bar = 10 mm; FIG. 147: Aperture of a single specimen surrounded by many recently settled juveniles. Scale bar = 1 mm; FIG. 148: SEM image of teleoconch sculpture after removal of encrusting coralline algae. Scale bar = 200 um; FIGS. 149-151: SEM images of protoconchs removed from recently settled juveniles. Scale bars = 100 um. FIG. 149: Abapertural view; FIG. 150: Apical view; FIG. 151: Detail of apical view showing sculpture; FIGS. 152-155: Opercula. Scale bars = 200 um. FIG. 152: Exterior surface; FIG. 153: Lateral view; FIG. 154: Interior surface; FIG. 155: SEM image of interior surface; FIG. 156: Central section of radula. Scale bar = 20 um.

“DENDROPOMA GROUP” WORM-SNAILS 45

Protoconch (Figs. 149-151): Settled proto-conch diameter to 410 um, height to 390 um. Sculpture absent on first 0.8 whorl, last 0.5 whorl with very low axial ribs crossed by numerous spiral bands of pustules near lip; one very weak spiral keel present. Dark brown.

Operculum (Figs. 152-155): Diameter to 1.5 mm. Domed, “mushroom-shaped”; dark burgundy with transparent margins. Lamina on exterior surface stacked. Interior surface concave, with moderately tall, conical mam-milla.

Radula (Fig. 156): Length of ribbon 750 um; up to 33 rows. Outer marginal tooth: one cusp on inner side.

External Morphology and Color. Color of speci-mens preserved in EtOH (modified from Keen & Morton, 1960): Head-foot black, snout gray; cephalic tentacles black at base, white at tip; pedal tentacles gray.

Pallial and Reproductive Anatomy: Not known.

Development and Ecology: six unstalked egg capsules per female; three embryos per capsule (Keen & Morton, 1960). Adults reef-building.

Comparative Remarks

Belonging to the “convex-operculate” group of Dendropoma. Distinguished by the presence of pustulose spiral ribs near the lip ofthe proto-conch. The microsculpture on the protoconch was not documented in the description of the species (Keen & Morton, 1960), but this detail is only visible using SEM (a technique which was not available to the original authors).

Taxonomic Remarks

The type locality for D. tholia is on the south-ern coastline of Mozambique. The examined material was collected 2,500 km north of the type locality, in Kenya. However, there are no other suitable names available for Den-dropoma species from east Africa, except D. corallinaceum (Tomlin, 1939), which accord-ingt o Keen & Morton (1960) does not extend beyond East London on the southeast coast of South Africa.

The shell, operculum and radula of the ex-amined material agree in most respects with the description of D. tholia (Keen & Morton, 1960), supporting the tentative assignment of this material to D. tholia.

Distribution (Fig. 7)

East Africa, at least between Mozambique and Kenya.

Dendropoma expolitum n. sp.

Type Locality

Moderately exposed granite shore, Bampfield Pt., W side of Prince of Wales Island, Tor-res Strait, Queensland, Australia: 10.717°S, 142 117 E.

Material Examined

Australia: Holotype: QM MO.80207: coll. W. F. Ponder & I. Loch, July 1, 1976, 10% SW formalin (1 specimen attached to paratypes; Figs. 156, 157); Paratypes: AM C.464306, QM MO.80208, FMNH 328513, ex AM C.464306: from type locality, coll. W. F. Ponder & I. Loch, July 1, 1976, 10% SW formalin (many); AM C.154222: exposed rocky shore, LT, S side of Fly Point, Cape York Peninsula, Queensland, 10.75°S, 142.6°E, coll. W. F. Ponder& I. Loch, July 11, 1976, 10% SW formalin (many); AM C.464377: attached to bivalve shell, on beach, Frederick Reefs, Coral Sea, 21°S, 154.433°E, coll. K. Gillett, August 1972, dry (many).

Etymology

From the Latin adjective expolitus-a-um, meaning polished, referring to the features of the unsculptured protoconch.

Description

Teleoconch (Figs. 157-159): Apertural diameter to 2.0 mm (Keen & Morton, 1960); shell length to 6 mm, diameter of last whorl to 5 mm. Up to four whorls coiled concentrically; deeply entrenched in substratum; aperture flush with substratum; scars from abandoned feed-ing tubes absent. Exterior surface medium brown; sculpture of moderately tall, upright, coarse transverse lamellae; longitudinal crest absent. Interior surface dark brown.

46 GOLDING ET AL.

Protoconch (Figs. 160, 161): Settled proto- burgundy with transparent margins. Lamina
conch diameter to 400 um, height to 420 on exterior surface stacked. Interior surface
um. Sculpture absent; spiral keels absent. concave, with very low, conical mammilla.
Pale brown.
Radula (Fig. 167): Length of ribbon 1.0 mm; up
Operculum (Figs. 162-166): Diameter to 1.5 to 30 rows. Outer marginal tooth: two cusps
mm. Domed, “mushroom-shaped”; dark on inner side.

FIGS. 157-167. Dendropoma expolitum n. sp. FIG. 157: A cluster of specimens including holotype (marked with an asterisk) removed from the substratum, partly encrusted with coralline algae. AM C.464306, Prince of Wales Island, Torres Strait, Australia. Scale bar = 5 mm; FIG. 158: Holotype. QM MO.80207, Prince of Wales Island, Torres Strait. Scale bar = 1 mm; FIG. 159: SEM image of teleoconch sculpture. AM C.464306, Prince of Wales Island, Torres Strait, Australia. Scale bar = 200 um; FIGS. 160, 161: SEM images of protoconchs removed from recently-settled juveniles. АМ C.154222, Ну Point, Cape York, Australia. Scale bars = 100 um. FIG. 160: Abapertural view; FIG. 161: Detail of protoconch sculpture; FIG. 162: SEM image of lateral view of operculum. AM C.464306, Prince of Wales Island, Torres Strait. Scale bar = 500 um; FIGS. 163-166: Opercula. AM C.154222, Fly Point, Cape York, Australia. Scale bars = 500 um. FIG. 163: SEM image of oblique view of interior surface; FIG. 164: Exterior surface; FIG. 165: Lateral view; FIG. 166: Interior surface; FIG. 167: Central section of radula. AM C.464306, Prince of Wales Island, Torres Strait, Australia. Scale bar = 20 um.

“РЕМОКОРОМА GROUP” WORM-SNAILS 47

FIGS. 168-170. Anatomy of Dendropoma expolitum n. sp. FIG. 168: Left view of female specimen. AM C.464306. Prince of Wales Island, Torres Strait, Australia. Scale bar = 1 mm; FIG. 169: Mantle cavity of female specimen, showing pallial oviduct. AM C.154222, Fly Point, Cape York, Australia. Scale bar = 1 mm; FIG. 170: Pallial vas deferens. AM C.464306, Prince of Wales Island, Torres Strait, Australia. Scale bar = 500 um.

External Morphology and Color (Fig. 168): Body
slender, length to 25 mm; occupying 2-3
whorls of shell. Columellar muscle extending
one whorl. Color of specimens preserved in
70% EtOH: Colorless except for pale gray pigment on dorsal surface of head and black pigment at base of tentacles.

Pallial and Reproductive Anatomy (Figs. 169, 170): Gill with 17 leaflets per mm. Osphradium short, 1.2 mm long; anterior tip straight. Rectum kinked. Hypobranchial

gland not extending across rectum. Pallial oviduct without notch at midpoint or proximal diverticulum.

Development and Ecology: Developmental biology not known. Adults reef-building.

Comparative Remarks

Belonging to the “convex-operculate” group of Dendropoma. Distinguished by its unsculptured protoconch.

48 GOLDING ET AL.

Taxonomic Remarks

Dendropoma expolitum n. sp. is morphologi-
cally consistent from each locality here studied.

Distribution (Fig. 7)

Known from northeast Australia between the
central Great Barrier Reef and Cape York.

Novastoa
Finlay, 1926

Novastoa Finlay, 1926: 386; Morton, 1951: 43-51, plate 8, figs. 1, 2, 4b, plate 9, figs 5, 6, text-fig. 1; Bieler & Petit, 2011: 16. Dendropoma (Novastoa) — Keen, 1961: 199- 200, text-figs. 30-33.

Type Species

Siphonium lamellosum Hutton, 1873, by original designation.

Diagnostic Description

Teleoconch: Small to medium (maximum di-mension 4-28 mm), “tube” wide (apertural diameter 2.3-7.5 mm), sometimes with expanded chamber behind aperture; whorl coiling pattern concentric spiral sometimes tending to straight, shallowly or deeply entrenched or entirely embedded in sub-stratum initially but sometimes elevated in later whorls; aperture flush with substratum or elevated, usually not forming a feeding tube; encrusted or entirely camouflaged with epifauna. Shell thick or thin; aperture simple. Color and sculpture of exterior surface vari-able. Interior surface color variable; sculpture on columellar surface absent; concave septa frequent in abandoned shell.

Protoconch: Settled protoconch diameter 600-1100 um, height 500-1000 um. Weak “hook” projection present on apertural lip. In-tracapsular growth only evident in protoconch structure; globular with large increase in whorl size; shallow suture; 1.3 whorls; sculpture variable; spiral keels at base of whorl absent. Color variable, transparent.

Operculum: Circular in axial profile; diam-eter proportional to shell size, 1.5-6.0 mm. Composed of chitin only; color variable. Exterior surface concave, either shallow saucer-shaped or shallow to deeply conical in

lateral profile (excluding mammilla). Exterior surface with tall, upright, multispiral lamina, usually heavily encrusted with epifauna. In-terior surface with a prominent mammilla of varying height and profile; surface glossy and smooth peripherally, muscle attachment area (including mammilla) textured with shallow concentric grooves.

Radula: Taenioglossate, transparent, color-less. Length of ribbon 730-2500 um; 23-44 rows (proportional to shell size). Trapezoidal rachidian tooth with prominent central cusp flanked on each side by three smaller cusps decreasing in size outwardly. Base of lateral tooth notched to interlock with rachidian and inner marginal teeth; elongate main cusp flanked by one cusp on inner side, three cusps on outer side. Inner marginal tooth slender with one cusp on inner side, 2—3 cusps on outer side. Outer marginal tooth smooth on outer side, one cusp on inner side; base simple, without projection.

External Morphology and Color. Body of animal usually very stout (length 7-40 mm), occupy-ing between 1 and 2 last whorls of shell; 0.5x body length composed of gonad and diges-tive gland. Columellar muscle medium length to very short, extending between 1 and 0.5 whorls. Pedal tentacles short (in preserved specimens). Head relatively large, cephalic tentacles short (in preserved specimens), broad, with tiny ommatophore bearing eye at outer base; right side of head with deep food groove sometimes with convoluted flap on outer margin. Adult female mantle divided by pallial slit (0.5x mantle length) or notch (< 0.3x mantle length) in midline; male mantle undi-vided. External body coloration variable.

Pallial and Reproductive Anatomy: Gill 0.2—0.3x mantle width, full length of mantle cavity; gill leaflets medium height to tall triangular; 12-16 leaflets per mm. Osphradium short or long relative to mantle cavity, 2.5-5.3 mm; margins irregular or smooth; anteriotri p bent 180° or curved towards columellar muscle. Anus either opening within mantle cavity or protruding from mantle aperture; rectum kinked; fecal pellets ovoid or cigar shaped. Hypobranchial gland pale brown (if visible), covering surface of mantle between gill and rectum, sometimes also covering rectum and pallial oviduct. Pallial oviduct notched near midpoint with expanded pocket distal to notch; proximal diverticulum present. Single

“DENDROPOMA GROUP” WORM-SNAILS 49

seminal receptacle attached to base or tip of proximal diverticulum via short duct. Male reproductive system sometimes with notch near midpoint of pallial vas deferens.

Development and Ecology: (At least) 1-5 stalked egg capsules attached to shell wall in a single row corresponding to position of mantle slit/notch in females; double-walled capsule semi-transparent, elongate ovoid to kidney shaped, diameter increasing with development ofembryos, size of capsule and number of eggs/embryos per capsule varying between species. Larvae probably direct de-veloping. Adults solitary or gregarious, some species reef-building.

Comparative Remarks

The slit female mantle and method of (stalked) capsule attachment are shared with Cupolaconcha, Ceraesignum and most mem-bers of other vermetid genera. Novastoa can be distinguished from these other vermetids by the distinct operculum that has a prominent mammilla on the interior surface (developed to a remarkable degreei n some taxa) and a raised, multispiral lamina on the exterior sur-face of the operculum.

Taxonomic Remarks

Novastoa was introduced by Finlay (1926) at the generic level for N. lamellosa, but sub-sequently reduced to a subgenus of Dendro-poma by Keen (1961). Keen (1961) provided a diagnosis for the subgenus that conflates some of the features described by Morton (1951) from N. lamellosa with those of other, unrelated, Dendropoma species, such as an aggregate growth habit and a short spindle on the interior surface of the operculum. The operculum figured by Keen (1961) is redrawn from Morton (1951) but does not closely re-semble his description or our own. Keen (1961) included many other species in D. (Novastoa). Of those examined in this study, none appear to belong in Novastoa and mostly are members of Dendropoma proper.

Diversity and Distribution (Fig. 171)

Present in all oceans except the Arctic, gener-ally tropical but also known from temperature waters in New Zealand. Six species, including one previously named species, are described

below. This is almost certainly an underesti-mate of the real diversity of Novastoa, as the small, deeply embedded shells of several taxa are extremely cryptic and difficult to collect from their reef habitat.

Novastoa lamellosa
(Hutton, 1873)

Siphonium lamellosum Hutton, 1873: 30; Bieler & Petit, 2011: 43.
Novastoa lamellosa — Finlay, 1926: 386; Mor-ton, 1951: 43-51, pl. 8 figs. 1, 2, 4b, pl. 9 figs. 5, 6, text-fig. 1; 1955: 4 ff., fig. 1a, b. Dendropoma (Novastoa) lamellosum — Keen, 1961: 199-200, text-figs. 30-33; Morton, 1965: 588 ff., fig. 3 [gross anatomy, opercu-lum; as О. lamellosa].

Type Locality

New Zealand, precise locality unknown. Given as “Cook Strait, in deep water” by Suter (1913: 261) and “Chatham Islands” by Powell (1979: 129).

Material Examined

New Zealand: Syntypes (photograph): NMNZ M.000133 [http://collections.tepapa.govt. nz/objectdetails.aspx?oid=753150]. Other: NMNZ M.012245: Kaingaroa, Chatham Islands, 43.73°S, 176.23°W, coll. R. K. Dell, January 27, 1954, 80% EtOH (many), dry (many); NMNZ M.024381: Great Island, Southeast Bay, Three Kings Islands, 34.17°S, 172.13°E, coll. F. Climo, November 28, 1970, 80% EtOH (many), dry (many); NMNZ M.004786: rock face exposed to swell, Noises Islands, Hauraki Gulf, North Island, 36.70°S, 174.97°E, coll. L. Moore, May 1, 1938, dry (many).

Description

Teleoconch (Figs. 172-174): Apertural diam-etert o 7.5 mm, without an expanded chamber behind aperture; diameter of last whorl to 28 mm. Up to six whorls coiled concentrically, tending to straight in later whorls; early whorls deeply entrenched in substratum; aperture raised above substratum in some dense colonies. Shell thick. Exterior surface purple fading to white; sculpture of tall, delicate, transverse lamellae. Interior surface white with brown patches.

50 GOLDING ET AL.

FIG. 171. Distribution map of Novastoa Finlay, 1926 based on material examined in this study. Filled diamond = N. lamellosa (Hutton, 1873); hollow diamond = N. caboverdensis n. sp.; filled circle = N. bahamensis п. sp.; filled square = N. pholetor n. sp.; hollow square = N. batavia п. sp.; filled triangle = №. sp.

Protoconch (Figs. 175, 176): Settled and hatch-
ling protoconch diametert o 1,100 um, height
to 1,000 um. Sculpture absent on first whorl,
last 0.3 whorl with many wavy, spiral bands of
pustules joining to form broken threads near lip. White to pale brown.

Operculum (Figs. 177-181): Diametert o 6 mm. Shallow saucer-shaped; dark caramel brown. Lamina on exterior surface not ruffled. Interior surface with tall, cylindrical mammilla up to 2.5 mm long.

Radula (Fig. 182): Length of ribbon 2.5 mm; up to 34 rows.

External Morphology and Color (Figs. 183, 184): Body length to 40 mm, occupying last two whorls of shell. Columellar muscle medium length, extending one whorl within shell. Food groove with simple outer margin. Adult female mantle divided by pallial slit extending 0.5x mantle length. Color in life (modified from Mor-ton, 1951): dorsal surface of head jet black, lips orange, snout scarlet, cheeks with black patches; cephalic tentacles black with yellow patches near base; pedal tentacles black; foot whitish posteriorly with lateral black patches and orange-brown in food groove; remnant

sole of foot orange-red; mantle margin with thin black band, canary yellow then scarlet fading to translucent white. Color ofspecimens preserved in 80% EtOH: head/foot cream; sides of foot pale grey; pedal and cephalic tentacles black; dorsal surface of head with circular patch of black pigment; mantle edge of mantle grey with band of white pigment on margin; digestive gland faded to cream.

Pallial and Reproductive Anatomy (Figs. 185- 187): Gill 0.2x mantle width; gill leaflets tall triangular, breadth half height; 12 leaflets per mm. Osphradium short, 3 mm long; margins irregular; anterior tip curved towards columel-lar muscle. Anus opening within mantle cav-ity; fecal pellets not observed. Hypobranchial gland pale brown, covering surface of mantle between gill and extending across rectum and ventral surface of pallial oviduct. Seminal receptacle attached to tip of proximal oviduct. Male reproductive system not observed.

Development and Ecology (Fig. 188): Up to ten stalked egg capsules per female; 6-16 embryos per capsule; up to 2.2 mm diameter. Larval biol-ogy not known, but intracapsular larval shells same size as settled protoconchs removed from substratum around adults, suggesting direct de-

“DENDROPOMA GROUP” WORM-SNAILS 51

velopment. Adults densely aggregated, forming crusts and reefs on rocky substratum.

Comparative Remarks

Distinct from other vermetids and species in Novastoa by the purple shell, presence of very talltransverse lamellae on the teleoconch and a tall, cylindrical mammilla on the interior surface of the operculum.

Taxonomic Remarks

The description here concurs in most re-spects with the detailed descriptions given by Morton (1951, 1965) and the material examined
is almost certainly conspecific. There are a
few differences, notably that Morton (1951)
did not describe a raised, multispiral lamina
on the exterior surface of the operculum. This
might have been inadvertently removed when

FIGS. 172-182. Novastoa lamellosa (Hutton, 1873). FIG. 172: Cluster of specimens. NMNZ M.004786, Noises Islands, New Zealand. Scale bar = 10 mm; FIG. 173: Adult shell attached to substratum. NMNZ M.024381, Three Kings Islands, New Zealand. Scale bar = 5 mm; FIG. 174: SEM image of teleoconch sculpture. NMNZ M.024381, Three Kings Islands, New Zealand. Scale bar = 500 um, FIGS. 175, 176: SEM images of protoconch. NMNZ M.012245, Chatham Islands, New Zealand; FIG. 175: Abapertural view. Scale bar = 200 um, FIG. 176: Detail of sculpture. Scale bar = 100 um; FIGS. 177-179: Operculum. NMNZ M.024381, Three Kings Islands, New Zealand. Scale bar = 500 um. FIG. 177: Exterior surface; FIG. 178: Lateral view; FIG. 179: Interior surface; FIG. 180: SEM image of exterior surface of opercu-lum. NMNZ M.012245, Chatham Islands, New Zealand. Scale bar = 500 um; FIG. 181: SEM image of oblique view of mammilla on interior surface of operculum. NMNZ M.024381, Three Kings Islands, New Zealand. Scale bar = 500 um; FIG. 182: Central section of radula. NMNZ M.012245, Chatham Islands, New Zealand. Scale bar = 50 um.

92 GOLDING ET AL.

FIGS. 183-188. Novastoa lamellosa (Hutton, 1873). NMNZ M.012245, Chatham Islands, New Zea-land. FIG. 183: Left view of female specimen. Scale bar = 5 mm; FIG. 184: Dorsal view of anterior body of male specimen. Scale bar = 1 mm; FIG. 185: Mantle cavity of female specimen. Scale bar = 5 mm; FIG. 186: Pallial oviduct. Scale bar = 2 mm; FIG. 187: Gill leaflet. Scale bar = 500 um; FIG. 188: Stalked egg capsule at late stage of development. Scale bar = 1 mm.

cleaning the operculum to remove encrusting
algae. Morton (1951) also did not describe the
delicate spiral sculpture on the protoconch, but
this is not visible without SEM. The material
examined here agreed with Morton’s (1951)
observation of a slit female mantle, but not with his later conclusion that the female mantle is entire (Morton, 1965).

Distribution (Fig. 171)

Known from New Zealand. Examined mate-rial from several locations on the North Island of New Zealand and remote islands northwest

(Three Kings Islands) and southeast (Chatham Islands) of New Zealand.

Novastoa caboverdensis n. sp.

Type Locality

Rocky littoral, Pedra Lume, Sal, Republic of the Cape Verde Islands: 16.45°N, 22.53°W.

Material Examined

Holotype: FMNH 301978: from type local-ity, coll. I. Kappner & K. Defren, April 22,

“DENDROPOMA GROUP” WORM-SNAILS 53

2003, 95% EtOH (1 male specimen) [DNA sequence data].

Etymology

Named after the type locality in the island nation of Cape Verde (Cabo Verde). Adjective in genitive case.

Description

Teleoconch (Figs. 189, 190): Apertural diam-eter 5.7 mm, not expanded behind aperture; diameter of last whorl 16 mm. Four whorls coiled concentrically; shallowly entrenched in substratum; aperture flush with substra-tum. Shell thick. Exterior surface cream with irregular brown discoloration; sculpture of thick, transverse, ruffled lamellae forming approximately 14 longitudinal ribs. Interior surface white with irregular brown patches.

Protoconch: Not known.

Operculum (Figs. 191-194): Diameter 4.9 mm. Shallow conical; bright orange around muscle

attachment area fading to white peripherally. Lamina on exterior surface ruffled. Interior surface with short conical to nipple-shaped mammilla.

Radula (Fig. 195): Length of ribbon 2.5 mm, width 320 um; 44 rows.

External Morphology and Color (Fig. 196): Body length 19 mm, occupying last whorl of shell. Columellar muscle medium length, extending one whorl. Food groove with simple outer margin. Adult female morphology not observed. Color of holotype specimen pre-served in 95% EtOH: head/foot white with mottled grey pigment on dorsal and lateral surfaces of head and anterior margin of foot; pedal and cephalic tentacles white; mantle margin dark grey with white trim; digestive gland pale brown.

Pallial and Reproductive Anatomy (Figs.
197-199): Gill 0.2x mantle width; gill leaflets
medium height triangular, breadth equal to
height; 14 leaflets per mm. Osphradium long,
5.3 mm; margins smooth; anterior tip curved

à 191

FIGS. 189-195. Holotype of Novastoa caboverdensis n. sp. FMNH 301978, Pedra Lume, Cape Verde. FIG. 189: Shell removed from substratum. Scale bar = 5 mm; FIG. 190: SEM image of teleoconch sculp-ture. Scale bar = 500 um; FIGS. 191-193: Operculum. Scale bar = 1 mm. FIG. 191: Exterior surface; FIG. 192: Lateral view; FIG. 193: Interior surface; FIG. 194: SEM image of muscle attachment area on interior surface of operculum. Scale bar = 500 um; FIG. 195: Central section of radula. Scale bar = 100 um.

54 GOLDING ET AL.

FIGS. 196-199. Anatomy of male holotype of Novastoa caboverdensis n. sp. FMNH 301978, Pedra Lume, Cape Verde. FIG. 196: Body of male. Scale bar = 2 mm; FIG. 197: Mantle cavity of male. Scale bar =2 mm; FIG. 198: Gill leaflet from mid-section of gill. Scale bar = 500 um; FIG. 199: Pallial vas deferens. Scale bar = 1 mm.

towards columellar muscle. Anus opening
within mantle cavity; fecal pellets cigar-
shaped. Hypobranchial gland pale brown,
covering surface of mantle between gill and
rectum, covering part of rectum. Female re-productive system not observed. Pallial vas deferens notched near midpoint.

Developmenatnd Ecology: Egg capsule morphol-ogy and larval biology unknown. Single adult specimen collected, but ecology not known.

Comparative Remarks

Somewhat similar in shell and soft-tissue mor-phology to N. lamellosa, but lacking a cylindrical mammilla on the interior surface of the opercu-lum. Dendropoma marchadi Keen & Morton, 1960, occurs nearby in Senegal on mainland Africa. These species can be distinguished by the much larger shell of N. caboverdensis n. sp. and the presence of a raised, multispiral, ruffled lamina on the exterior surface of the

“DENDROPOMA GROUP” WORM-SNAILS 55

operculum. Dendropoma marchadi is known to brood unstalked egg capsules within the mantle cavity. The brooding behavior of N. cabover-densis n. sp. is not known, but may be similar to other species of Novastoa that attach stalked egg capsules to the shell wall.

Distribution (Fig. 171)

Known only from a single specimen from the type locality at Pedra Lume on the island of Sal in Cape Verde.

Novastoa bahamensis n. sp.

Type Locality

Intertidal zone, Silver Point, Grand Bahama
Island, The Bahamas: 26.50°N, 78.66°W.

Material Examined

Bahamas: Holotype: FMNH 329355, coll. J. Wors-
fold, January 8, 1989, 70% EtOH (1 specimen);
Paratypes: FMNH 329356, from the type local-

FIGS. 200-210. Novastoa bahamensis n. sp. FIGS. 200, 201: Part of holotype shell. FMNH 329355, Grand Bahama Island, Bahamas. Scale bar = 5 mm. FIG. 200: Exterior of shell fragment; FIG. 201: Interior of shell fragment; FIGS. 202, 203: Paratype shell. FMNH 329356, Grand Bahama Island, Ba-hamas. FIG. 202: Exterior of shell. Scale bar = 2 mm; FIG. 203: SEM image of teleoconch sculpture. Scale bar = 500 um; FIGS. 204—208: Operculum. FMNH 329356. Scale bar = 1 mm. FIG. 204: SEM of exterior surface; FIG. 205: SEM of interior surface; FIG. 206: Exterior surface; FIG. 207: Lateral view; FIG. 208: Interior surface; FIG. 209: SEM image of muscle attachment area on interior surface. FMNH 329356. Scale bar = 500 um; FIG. 210: Central section of radula. FMNH 329356. Scale bar = 50 um.

56 GOLDING ET AL.

ity, coll. J. Worsfold, January 8, 1989, 70% EtOH Creek, Andros Island, 24.7345°N, 77.7928°W,
(1 specimen); FMNH 327205, oolitic limestone coll. T. Rawlings, March 26, 2004, 95% EtOH
platform in front of Point of View Villas, Fresh (5 specimens) [DNA sequence data].

c| t MO pt

FIGS. 211-215. Anatomy of Novastoa bahamensis n. sp. FIG. 211: Body of male holotype. FMNH 329355, Grand Bahama Island, Bahamas. Scale bar = 2 mm; FIG. 212: Dorsal view of anterior body, female. FMNH 327205, Andros Island, Bahamas. Scale bar = 1 mm; FIG. 213: Mantle cavity of male holotype. FMNH 329355. Grand Bahama Island, Bahamas. Scale bar = 2 mm; FIG. 214: Gill leaflets from mid and anterior sections of gill. FMNH 327205. Scale bar = 500 um; FIG. 215: Pallial oviduct with ventral surface of expanded pocket peeled back. Paratype, FMNH 329356, Grand Bahama Island, Bahamas. Scale bar = 1 mm.

“DENDROPOMA GROUP” WORM-SNAILS 57

Etymology

Named for its occurrence in the Bahamas (adjective). |

Description

Teleoconch (Figs. 200-203): Apertural diam-eter to 6.6 mm, not expanded behind ap-erture; diameter of last whorl to 17 mm. Up to four whorls coiled concentrically; deeply entrenched in substratum; aperture flush with substratum. Shell thick. Exterior surface white; sculpture of closely-packed, upright, ruffled, transverse lamellae (often heavily worn). Interior surface white with irregular burgundy patches.

Protoconch: Not known.

Operculum (Figs. 204-209): Diameter to 4.2 mm. Shallow saucer-shaped; peripherally white with golden yellow muscle attachment area on interior surface. Lamina on exterior surface ruffled. Interior surface with short, conical mammilla. |

Кади (Fig. 210): Lengthof ribbon to 2.3 mm, width to 275 um; up to 45 rows.

External Morphology and Color (Figs. 211, 212): Body length to 19 mm, occupying last whorl of shell. Columellar muscle very short, extending < 0.5 whorl. Food groove with convoluted flap on outer margin. Adult female mantle divided by pallial notch extending < 0.3x mantle length. Color of specimens preserved in 70% EtOH: pedal and cephalic tentacles white; head-foot white with mottled grey pigment on sides of foot and dorsal surface of head; mantle dark grey.

Pallial and Reproductive Anatomy (Figs. 213-215): Gill 0.2x mantle width; gill leaflets moderate height triangular, breadth equal to height; 12 leaflets per mm. Osphradium short, 2.5 mm; margins smooth; anterior tip curved towards columellar muscle. Anus opening within mantle cavity; fecal pellets ovoid. Hy-pobranchial gland pale brown, covering sur-face of mantle between gill and rectum only. Seminal receptacle attached to tip of proximal diverticulum from pallial oviduct. Pallial vas deferens without notch near midpoint.

Developmenatnd Ecology (Fig. 214): Egg cap-sule morphology and larval biology unknown.

Solitary adults living on vertical rock surfaces in intertidal zone. |

Comparative Remarks

Superficially similar, in life, to Dendropoma nebulosum and Novastoa pholetor n. sp., both of which also occur in the Caribbean. Novastoa bahamensis n. sp. occurs on rocks in the intertidal zone, while D. nebulosum is found in deeper water (SCUBA depth). Also, the head pigmentation and opercular morphology of N. bahamensis n. sp. are distinctive and the presence of stalked egg capsules is de-finitive in distinguishing these taxa. Novastoa bahamensis n. sp. can be distinguished from N. pholetor n. sp. by the operculum, which is white and yellow in N. bahamensis n. sp. but pink and red in N. pholetor n. sp. These taxa are closely related in the molecular phylogeny and share many morphological characters.

Distribution (Fig. 171)

Known only from two islands in the Bahamas.

Novastoa pholetor n. sp.

Type Locality

1.5 m depth, on coral rubble and living coral heads, Tobacco Reef, Stann Creek District, Belize: 16.8236°N, 88.0812°W.

Material Examined

Belize: Holotype: FMNH 328511, coll. R. Bieler, T. Collins, К. Golding, T. Rawlings - & P. Sierwald, April 22, 2011, 70% EtOH (1 specimen); Paratypes: FMNH 327177: from type locality; coll. R. Bieler, T. Collins, К. Golding, T. Rawlings & P. Sierwald, April 22, 2011, RNAlater (4 tissue samples), 95% EtOH (4 tissue samples and egg capsules), 3.5% glutaraldehyde (2 testes), 70% EtOH (many), 5% SW formalin (many), dry (shell fragments). FMNH 327160: 8 m on coral heads, Columbus Reef, Stann Creek District, Belize, 16.9028°N, 88.0554°W, coll. R. Bieler 8 P. Sierwald, April 18, 2011, RNAlater (1 tis-sue sample), 95% EtOH (1 tissue sample), 5% SW formalin (1 body and egg capsules), dry (shell fragments); ЕММН 327172: 1 топ surface of coral boulders covered with algal “lawn”, lagoon E of Carrie Bow Cay, Stann Creek District, 16.8027°N, 88.0816°W, coll.

58 GOLDING ET AL.

К. Bieler, T. Collins, R. Golding, T. Rawlings data]; FMNH 327181: 1 mon surface of coral
& P. Sierwald, April 21, 2011, RNAlater (2 tis- boulders covered with algal “lawn”, lagoon
sue samples), 95% EtOH (2 bodies without E of Carrie Bow Cay, Stann Creek District,
shells), dry (shell fragments), [DNA sequence 16.8027°N, 88.0816°W, coll. R. Bieler, T. Col-

FIGS. 216-228. Novastoa pholetor n. sp. FIG. 216: Specimen attached to substratum, partly covered by coralline algae. Paratype, FMNH 327177, Tobacco Reef, Belize. Scale bar = 5 mm; FIG. 217: Living specimen in situ embedded in substratum, with only aperture and heavily encrusted operculum visible (arrow). Paratype, FMNH 327177; FIG. 218: SEM image of teleoconch sculpture. Paratype, FMNH 327177. Scale bar = 1 mm; FIGS. 219-221: SEM images of intracapsular larval shells. Paratype, FMNH 327177. Scale bar = 100 um. FIG. 219: Abapertural view; FIG. 220: Apertural view; FIG. 221: Apical view; FIGS. 222, 223: SEM images of operculum. Paratype, FMNH 327177. Scale bar = 1 mm. FIG. 222: Exterior surface; FIG. 223: Interior surface; FIG. 224: Operculum removed from living animal with encrusted layer attached to exterior surface, lateral view. FMNH 327160, Columbus Reef, Belize. Scale bar = 1 mm; FIG. 225: Central section of radula. Paratype, FMNH 327177. Scale bar = 50 um; FIGS. 226, 227: Living specimen partially removed from shell. Paratype, FMNH 327177. FIG. 226: Female with stalked egg capsule exposed (arrow); FIG. 227: Pigmentation on the head and foot; FIG. 228: Stalked egg capsule containing late-stage embryos in two color morphs. FMNH 327160. Scale bar = 1 mm.

“DENDROPOMA GROUP” WORM-SNAILS 99

lins, R. Golding, T. Rawlings & P. Sierwald, April 24, 2011, 95% EtOH (1 specimen), 70% EtOH (1 specimen).

Etymology

Named for its deep-hidden, burrowed mode of life. The heavily encrusted operculum match-es the surrounding substratum, and when held slightly ajar to permit feeding resembles the camouflaged entrance to the burrow of a trap-door spider. From the Latin pholetor, for “one who Iurks in a hole” (noun in apposition).

Description

Teleoconch (Figs. 216-218): Apertural diam-eter to 6 mm, not expanded behind aper-ture; diameter of last whorl to 21 mm. Up to four whorls coiled concentrically; deeply entrenched in substratum (Sometimes en-tirely embedded with only aperture visible); aperture flush with substratum. Shell thick. Exterior surface white; sculpture of closely-packed, upright, ruffled, transverse lamellae (often heavily worn). Interior surface white with brown patches.

Protoconch (Figs. 219-221): Hatchling proto-conch diameter to 600 um, height to 500 um. Sculpture absent on first 0.6 whorl, last 0.7 whorl with very tall, widely-spaced axial ribs. Either white or dark brown, roughly equal proportions of each color occurring per egg capsule.

Operculum (Figs. 222-224): Diameter to 4.5 mm. Shallow conical; raspberry red periph-ery fading to pale pink muscle attachment area. Interior surface with short, conical mammilla.

Radula (Fig. 225): Length of ribbon to 2.1 mm, width to 275 um; up to 41 rows.

External Morphology and Color (Figs. 226, 227): Body length to 21 mm, occupying last whorl of shell. Columellar muscle very short, extending < 0.5 whorl. Food groove with convoluted flap on outer margin. Adult female mantle divided by pallial notch extending < 0.3x mantle length. Color in life: head-foot base color translucent white overlaid with mottled opaque black and white pigment and bright yellow speckles; pedal and cephalic tentacles and lips pale yellow; mantle cream with opaque black and white speckles on

lateral edges, anterior edge black with alter-nating white dots on margin; digestive gland black; ovary cream.

Pallial and Reproductive Anatomy: Not known.

Development and Ecology (Fig. 228): Up to five stalked egg capsules per female; 32-45 eggs/ embryos per capsule; up to 1.5 mm diameter. Larval biology not known, but hatchling larvae barely capable of swimming and velum mostly resorbed, suggesting direct development. Proportion of white and dark brown larvae per capsule roughly equal. Adults common in subtidal zone and behind wave-zone on reef crest. Solitary and extremely cryptic.

Comparative Remarks

Superficially similar, in life, to both Dendropo-ma nebulosum and Novastoa bahamensis п. sp., which have similar Caribbean distributions. Novastoa pholetor n. sp. generally occurs in shallow subtidal habitat in the wave zone, but N. bahamensis n. sp. occurs intertidally and D. nebulosum in deeper water (SCUBA depth). The head pigmentation and opercular morphol- . ogy of N. pholetor n. sp. are highly distinctive and the presence of stalked egg capsules prevents confusion between this species and D. nebulosum. Comparison with N. bahamensis n. sp. shows many morphological similarities, but these species are well-separated by mo-lecular data. They can also be distinguished by the color of the operculum.

Distribution (Fig. 171)

Known only from localities in the vicinity of Carrie Bow Cay, Belize.

Novastoa batavia n. sp.

Type Locality

On dead Acropora spp., 6-8 m by SCUBA, reef slope off main dock at Beacon Island station, Goss Channel, Wallabi Group, Hout-man Abrolhos, Western Australia, Australia: 28.7090°8, 113.78 75°E.

Material Examined

Western Australia: Holotype: WAM S66359 ex FMNH 329357 (Fig. 229): coll. R. Bieler, May 27, 1994, 70% EtOH (1 specimen); Paratypes: FMNH 327038: from type locality,

60 GOLDING ET AL.

coll. R. Bieler, May 27, 1994, 70% EtOH (4 specimens); FMNH 327047: very protected
water with layer of silt on hard bottom, among
Posidonia australis, W side of West Wallabi
Island, Wallabi Group, Houtman Abrolhos,
28.4523°S, 113.7023°E, coll. R. Bieler, May 19, 1994, 70% EtOH (2 specimens).

Etymology

Named for the Dutch East India Company vessel Batavia which was infamously ship-wrecked in 1629 near the type locality on Beacon Island, in the Houtman Abrolhos of Western Australia. Noun in apposition.

“DENDROPOMA GROUP” WORM-SNAILS 61

Description Radula (Fig. 242): Length of ribbon to 2.5 mm, width to 340 um; up to 43 rows. Teleoconch (Figs. 229-236): Apertural diameter
to 4.0 mm, diameter of expanded “chamber” External Morphology and Color (Figs. 233, 234, behind aperture to 6.3 mm; estimated diam-
eter of shell fragment from largest specimen
> 15 mm. Up to three whorls coiled concentri-
cally; entirely embedded in substratum with
only aperture and dorsal surface occasionally
exposed; aperture flush with surface. Shell thick on exposed dorsal surface but very thin on embedded surfaces. Exterior surface entirely surrounded by substratum matrix or encrusting epifauna, but when cleaned pale brown on exposed dorsal surface and white on embedded surfaces; sculpture of low, transverse lamellae. Interior surface white with transverse stripes of brown on columellar surface of last whorl (in “chamber”).

Protoconch (Fig. 237): Settled protoconch diameter (from partially obscured specimen) approx. 630 um, height 620 um. Sculpture on last 0.5 whorl of tall, widely-spaced axial ribs. Pale brown.

Operculum (Figs. 238-241): Diameter 4.9 mm. Deeply conical; pale golden mammilla surrounded by ring of dark orange fading to white peripherally. Lamina on exterior surface ruffled. Interior surface with short, nipple-shaped mammilla.

243-245): Body length to 13 mm, occupying last whorl of shell. Columellar muscle vary short, extending < 0.5 whorl. Food groove with convoluted flap on outer margin. Adult female mantle divided by pallial notch ex-tending < 0.3x mantle length. Color in life: head-foot strikingly mottled with opaque black and white pigment, black predominantly on forehead and around opercular lobe; cephalic tentacles white; forehead, anterior cheeks and mantle region bright yellow; pedal ten-tacles with black and white flecks, sometimes without black pigment; mantle margin with wide bright yellow band, remainder of mantle with black band interrupted by alternating large and small white patches. Color of specimens preserved in 70% EtOH: entirely white except for scattered flecks of black pig-ment on dorsal surface of head and around mantle margin.

Pallial and Reproductive Anatomy (Figs. 246-249): Gill 0.3x mantle width; gill leaflets moderate height, breadth equal to height;
14 leaflets per mm. Osphradium long, 5.0
mm; margins smooth; anterior tip bent 180°
around columellar muscle. Anus protruding
from mantle cavity; fecal pellets not observed.

do

FIGS. 229-242: Novastoa batavia n. sp. FIG. 229: Adult shell encrusted with coralline algae, only aperture visible. FMNH 327038, Beacon Island, Houtman Abrolhos, Australia. Scale bar =2 mm; FIG. 230: Juvenile shell and protoconch, not encrusted. FMNH 327038, Beacon Island, Houtman Abrolhos, Australia. Scale bar = 1 mm; FIG. 231: Ventral view of the holotype (female) occupying the “chamber” of its shell and showing a single stalked egg capsule attached to shell wall (indicated by an arrow). WAM S66359, Beacon Island, Houtman Abrolhos, Australia. Scale bar =2 mm; FIG. 232: SEM image, lateral view of shell deeply embedded in coral substratum, with lateral surface broken away to expose interior of “chamber” (right of image) and cross-section through narrowed aperture (indicated by an asterisk). FMNH 327038, Beacon Island, Houtman Abrolhos, Australia. Scale bar = 500 um; FIG. 233: Shell fragment showing coloration on interior surface. FMNH 327047, West Wallabi Island, Houtman Abrolhos, Australia. Scale bar =2 mm; FIG. 234: Lateral view of shell and animal removed from substra-tum, showing position of body in “chamber” below substratum surface. FMNH 327038, Beacon Island, Houtman Abrolhos, Australia. Scale bar = 1 mm; FIGS. 235, 236: SEM images shell surfaces. FMNH 327038, Beacon Island, Houtman Abrolhos, Australia. Scale bars = 200 um. FIG. 235: Teleoconch surface after removal of surrounding substratum; FIG. 236: Columellar surface of shell interior; FIG. 237: Abapertural view of protoconch surrounded by first whorl of adult shell. FMNH 327038, Beacon Island, Houtman Abrolhos, Australia. Scale bar = 200 um; FIG. 238: SEM image of muscle attachment area on interior surface of operculum. FMNH 327047, West Wallabi Island, Houtman Abrolhos, Aus-tralia. Scale bar = 500 um; FIGS. 239-241: Operculum. FMNH 327047, West Wallabi Island, Houtman Abrolhos, Australia. Scale bar = 1 mm. FIG. 239: Exterior surface; FIG. 240: Lateral view; FIG. 241: Interior surface; FIG. 242: Central section of radula. FMNH 327047, West Wallabi Island, Houtman Abrolhos, Australia. Scale bar = 50 um.

62 GOLDING ET AL.

FIGS. 243-250. Anatomy of Novastoa batavia n. sp. FIGS. 243, 244: Male specimen. Scale bars = 3 mm. FIG. 243: Right view; FIG. 244: Dorsal view of anterior body; FIG. 245: Dorsal view of anterior body of female holotype. WAM S66359, Beacon Island, Houtman Abrolhos, Australia. Scale bar = 1 mm; FIG. 246: Mantle cavity of female specimen. Scale bar = 2 mm; FIG. 247: Leaflet from mid-section of gill. Scale bar = 500 um; FIG. 248: Pallial oviduct. Scale bar = 1 mm; FIG. 249: Pallial vas deferens with ventral surface peeled back; FIG. 250: Egg capsule removed from holotype. WAM S66359, Beacon Island, Houtman Abrolhos, Australia. Scale bar = 500 um. FIGS. 243, 244, 246-250: FMNH 327047, West Wallabi Island, Houtman Abrolhos, Australia.

Hypobranchial gland not visible. Seminal not known. Adult ecology not known. Shell
receptacle attached to base of proximal and operculum often considerably fouled,
diverticulum from pallial oviduct. Pallial vas occasionally entirely embedded in coralline
deferens notched near midpoint. algae.

Development and Ecology (Figs. 231, 250): Comparative Remarks
Single female specimen observed with 1
stalked egg capsule; approx. 20 eggs per Most similar to Novastoa caboverdensis
capsule; diameter 1.2 mm. Larval biology n. sp. and N. pholetor n. sp., but operculum

“DENDROPOMA GROUP” WORM-SNAILS 63

is intense orange, rather than pale orange (N. caboverdensis) or pink (N. pholetor), around the muscle attachment area and more steeply concave.

Distribution (Fig. 171)

Known from two islands (Beacon and Wal-labi Islands) in the West Wallabi Group of the Houtman Abrolhos, in Western Australia. This is part of the most southerly coral reef on the coastline of Western Australia and is a unique habitat with many endemic species. The north-ern extent of the range is unknown.

Ceraesignum n. gen.

Dendropoma of authors [in part]. Non Dendro-poma Mörch, 1861.

Type species

Serpula maxima С. В. Sowerby |, 1825.

Etymology

From the Latin “cera” (= wax) and “signum” (= sign) for the texture on the interior surface of the operculum that resembles the impression of a fingerprint in wax. Noun of neuter gender in Latin.

Diagnostic Description

Teleoconch: Medium to large (maximum di-mension 15-450 mm), “tube” wide (apertural diameter 4.5-36 mm); whorl coiling pattern variable, deeply (or entirely) embedded in substratum (living coral or rock); aperture flush with substratum, not forming a feeding tube; encrusted with epifauna or covered by living coral. Shell thick; aperture simple. Color and sculpture of exterior surface variable. Interior surface color variable; sculpture on columellar surface absent; concave septa frequent in abandoned shell.

Protoconch: Settled protoconch diameter 370-700 um, height 420-710 um. “Hook” projection present from apertural lip, weak or strong. Intracapsular growth only evident in protoconch structure; globular with varying whorl proportions; 1.25-1.75 whorls; sculp-ture absent or present as axial and transverse ribs; spiral keels at base of whorl absent or present. Color variable, transparent.

Operculum: Circular in axial profile; diameter proportional to shell size, 2.3-40 mm. Com-posed of chitin only; transparent, brown. Deep to shallow concave saucer-shaped in lateral profile; without mammilla. Exterior surface sometimes encrusted with epifauna, smooth. Interior surface glossy, smooth except for muscle attachment area textured with “fingerprint” pattern of concentric ridges of varying height.

Radula: Taenioglossate, transparent, colorless or brown. Length of ribbon 2.1—6.5 тт; 49-60 rows (proportional to shell size). Trapezoidal rachidian tooth with prominent central cusp flanked on each side by three smaller cusps decreasing in size outwardly. Base of lateral tooth notched to interlock with rachidian and inner marginal teeth; elongate main cusp flanked by variable number of cusps on inner and outer sides. Inner marginal tooth slender with variable number of cusps on inner and outer sides. Outer marginal tooth smooth on outer side, 1-2 tiny triangular cusps on inner side, base simple, without projection.

External Morphology and Color. Body of animal stout (length 2.8-10 cm in examined wet ma-terial), occupying last half of shell (2 whorls | where coiled); 0.5x body length (earliest 1 whorl where coiled) composed of gonad and digestive gland. Columellar muscle very short, extending < 0.75 whorls. Pedal tentacles short (in preserved specimens). Head slightly bulbous, cephalic tentacles short (in preserved specimens), broad, with tiny ommatophore bearing eye at outer base; right side of head with food groove some-times present. Adult female mantle (all large specimens) divided by pallial slit, slightly left of midline; male mantle undivided. External body coloration variable.

Pallial and Reproductive Anatomy: Gill 0.2-0.3x mantle width, full length of mantle cavity; gill leaflets tall or short triangular; 7-16 leaflets per mm. Osphradium short relative to mantle cavity, 1.5-9.0 mm; margins irregular or smooth; anterior tip curled towards columel-lar muscle. Rectum running from coelom to anterior right edge of mantle cavity in deep curve; fecal pellets ovoid to cigar-shaped. Hypobranchial gland transparent brown to pale yellow, covering mantle surface between gill and rectum, also surface of rectum except tip, and sometimes surface of pallial oviduct.

64 GOLDING ET AL.

FIG. 251. Distribution map of Ceraesignum n. gen. based on material examined in this study and reports in the literature. Filled diamond = C. maximum (G. B. Sowerby |, 1825) locations for samples examined during this study; hollow diamond = C. maximum reports in the literature; filled square = C. robinsoncrusoein. sp.

Posterior end of pallial oviduct broad, taper-
ing to narrow strip anteriorly; proximal diver-
ticulum absent. Seminal receptacles absent
(not found in examined specimens). Male
reproductive system not examined.

Development and Ecology: 3-58 stalked egg capsules attached to shell wall in single row corresponding to position of mantle slit in females; double-walled capsule semi-transparent, elongate ovoid, diameter in-creasing with development of embryos, size of capsule and number of eggs/embryos per capsule varying between species. Probably protandric. Larval biology varying between species. Adults solitary or living in close proximity to each other.

Comparative Remarks

Like Cupolaconcha n. gen., Novastoa, and several other vermetid genera, members of Ceraesignum have stalked egg capsules at-tached to the shell wall through the divided female mantle. The animal of Ceraesignum is distinct in its saucer-shaped operculum (without a spiral lamina on the external surface

or mammilla on the internal surface, but with distinctive “thumbprint” surface texture) and simple, tapering pallial oviduct without obvious seminal receptacle or diverticulum.

Taxonomic Remarks

The type species, Serpula maxima, was histor-ically grouped with other large-shelled species (that today are mostly placed in Thylacodes), but never before separated into its own genus.

Diversity and Distribution (Fig. 251)

Ceraesignum n. gen. currently contains two species, one of which has been previously described. This low diversity may be genuine, or reflect the lack of knowledge of vermetid di-versity in general. There is a noticeable contrast between the distributions of each constituent species, with C. maximum widely distributed across the Indo-Pacific and C. robinsoncruso-ein. sp. restricted to a single remote, offshore island on the eastern rim of the Pacific Ocean. These contrasting demographics presumably reflect different life-history strategies and habi-tat tolerances/availability.

“DENDROPOMA GROUP” WORM-SNAILS 65

Ceraesignum maximum
(G. B. Sowerby I, 1825)
n. comb.

Serpula maxima G.B. Sowerby |, 1825: Ap-pendix p. i; Bieler & Petit, 2011: 46. Vermetus giganteus Quoy & Gaimard, 1834: 294-296, pl. 67 ["65”], figs. 13-15 [Guam]; Bieler & Petit, 2011: 38.
Siphonium maximum — Mörch, 1859: 354; 1861: 166-169; Clessin, 1902: 55-97. Siphonium giganteum “Quoy and Gaimond” [sic] - Clessin, 1902: 58 [with figs. after Quoy & Gaimard].
Vermetus novaehollandiae — Yonge, 1932: 259-281, figs. 1-6 (non Rousseau in Chenu, 1843).
Dendropoma (Dendropoma) maximum — Keen, 1961: 199; Morton, 1965: 588 ff., fig. 2 [gross anatomy, operculum; Queensland, Australia].
Dendropoma maxima — Kappner, 1998 [ecol-ogy, behavior; Gulf of Aqaba]; Kappner et al., 2000: 309 ff. [feeding; Gulf of Agaba]; Scaps & Denis, 2008: 1 ff., pl. 1 [indicator of coral reef status; Indonesia].
Dendropoma maximum — Hughes & Lewis, 1974: 531 ff. [ecology, reproduction; Red Sea]; Okutani, 2000: 207, pl. 103, figs. [Japan]; Raw-lings et al., 2001: 1605 [sequence and gene arrangement data; Gulf of Aqaba]; Phillips & Shima, 2010: 133 ff., figs. 1-4 [reproduction, larvae; French Polynesia]; Phillips, 2011: 2335 ff. [larval development; French Polynesia].

Type Locality

No locality given in original description. Keen (1961: 199) stated “East Indies”.

Material Examined

Original material studied by Mórch (1861: 166— 169), including his infrasubspecific forms “biangularis” and “praelonga” (NHMUK). Australia: AM C.326965: with coral in beach-rock gutter, SE side of North East Herald Cay, Coral Sea, 16.933°S; 149.183°E, coll. |. Loch, June 17, 1997, 10% SW formalin (1 female).
Republic of Kiribati: UF 410777: 10 m, outer reef slope, S of point S of main reef pas-sage, W side of Kiritimati Atoll, Line Islands, 1.8745°N, 157.5642°E, coll. G. Paulay, Au-gust 5, 2005, 95% EtOH (1 specimen). Guam, U.S.A.: UF 340207, Luminao Reef, Guam Island, Mariana Islands, 13.46°N,

144.65°E, coll. W. Kelly, May 16, 2003, 95% EtOH (1 male).
Cook Islands: UF291949: 0-2 m, Motutapu, Rarotonga Island, 21.24°S, 159.72°W, coll. C.P. Meyer, October 29, 2001, 95% EtOH (1 specimen), [DNA sequence даа].
French Polynesia: UF 401093: 0-2 m, in living Montipora, outer part of barrier reef between Cooks and Opunohu Bays, Moorea Island, Society Islands, 17.4772°S, 149.8306°W, coll. G. Paulay, July 2006, 75% EtOH (1 juvenile specimen); FMNH 327136: larvae cultured from females removed from coral, lagoon on the northeast shore of Moorea, 149.83°W, 17.5°S, coll. N. Phillips, April-September 2008, 70% EtOH (many larval shells). Japan: FMNH 328176: Ryukyu Islands, North Pacific Ocean, approx. 26°N, 127°E, coll. R. J. Rogers, 1953-1956, dry (shell fragment). New Zealand: FMNH 328251: Aitutaki Island, Cook Islands, South Pacific Ocean, approx. 19°S, 160°W, Chancellor-Stuart Field Muse-um Expedition, 1930, dry (shell fragment). Jordan: FMNH 318221: Marine Science Sta-tion, Gulf of Aqaba, Jordan, 29.4521°N, 24.9704°E, coll. |. Kappner, 1999, 95% EtOH (tissue only), [DNA sequence data].

Description

Teleoconch (Figs. 252-254): Apertural diam-eter to 3.6 cm (Yonge, 1932); shell length to 45 cm (Keen, 1961). Shell coiling for first few whorls, subsequent whorls irregular tending to straight, often orientated perpendicular to exposed surface of coral (Yonge, 1932). Exterior of shell rarely visible due to encrust-ing coral, but when exposed: exterior surface matt, white on columellar surface, pale fawn dorsally; sculpture varying from weak trans-verse striae to low, forward-sloping lamellae with thickened apical ridges. Interior surface white to cream, sometimes with diffuse, pale pink ring inside aperture.

Protoconch (Figs. 255, 256): Hatchling pro-toconch diameter to 370 um, height to 420 um. “Hook” projection weak. Globular, with small increase in whorl size; deep suture; 1.5-1.75 whorls; sculpture on first 0.75 whorl of pocked craters, last 0.75-1.0 whorl with widely-spaced, tall axial ribs crossed by > 20 spiral threads; 3 strong spiral keels present. Colorless.

Operculum (Figs. 257-260): Diameter to 40 mm (Yonge, 1932) (19 mm among examined

66

specimens). Shaped like a deep, concave saucer. “Fingerprint” texture on muscle attachment area composed of tall, closely-spaced, concentric ridges.

Radula (Fig. 261): Colorless to brown. Length of ribbon to 6.5 mm, width to 950 um, up to 60 rows. Lateral tooth: one cusp on inner side, five cusps on outer side. Inner marginal

GOLDING ET AL.

Head flat, small compared to foot muscle; food groove not visible. Color in life (based on Morton, 1965) and specimens preserved in 95% EtOH: head/foot, lips, tentacles cream to pale brown, sole and lateral surfaces of
foot, opercular lobe and dorsal surface of
head (excluding tentacles) ink black; anterior
mantle edge trimmed with cream then black
pigment bands; digestive gland dark brown.
tooth: two cusps on inner side, three cusps
on outer side. Pallial and Reproductive Anatomy (Figs. 263- 265): Gill 0.3x mantle width; gill leaflets trian-
gular, tall, height 5x breadth; seven leaflets per
mm. Osphradium 9 mm long; margins irregular.

External Morphology and Color (Fig. 262): Body
length to 10 mm (in examined specimens).

FIGS. 252-261. Ceraesignum maximum (С. В. Sowerby 1, 1825). FIG. 252: Aperture and mucous feeding net of animal living embedded in a coral head, Fiji. Photographed by W. F. Ponder; FIG. 253: Aperture of shell with surrounding coral partly removed. UF 410777, Kiritimati Atoll, Kiribati. Scale bar = 5 mm; FIG. 254: SEM image of teleoconch sculpture. UF 410777, Kiritimati Atoll, Kiribati; FIGS. 255, 256: Intracapsular larval shells. FMNH 327136, Moorea, French Polynesia. Scale bars = 50 um. FIG. 255: Abapertural view; FIG. 256: Apical view; FIGS. 257-259: Operculum. AM C.325965, Herald Cays, Coral Sea. Scale bar = 5 mm. FIG. 257: Exterior surface; FIG. 258: Lateral view; FIG. 259: Interior surface; FIG. 260: SEM image of sculpture on muscle attachment area on interior surface of operculum. AM C.325965, Herald Cays, Coral Sea. Scale bar = 500 um; FIG. 261: Central section of radula. AM C.325965, Herald Cays, Coral Sea. Scale bar = 200 um.

“DENDROPOMA GROUP” WORM-SNAILS 67

FIGS. 262-266. Anatomy of Ceraesignum maximum (С. В. Sowerby I, 1825). FIG. 262: Body of a small specimen, possibly male. UF 340207, Guam. Scale bar = 5 mm; FIG. 263: Anterior body and mantle cavity of female. AM C.325965, Herald Cay, Coral Sea. Scale bar = 20 mm; FIG. 264: Gill leaflet. UF340207, Guam. Scale bar = 500 um; FIG. 265: Pallial oviduct. AM C.325965, Herald Cay, Coral Sea. Scale bar = 5 mm; FIG. 266: Stalked egg capsule containing embryos at an early stage of development. Redrawn from Hughes & Lewis (1974), Plate 1c. Scale bar = 1 mm.

Fecal pellets cigar-shaped. Hypobranchial
gland pale yellow, not covering pallial oviduct.

Development and Ecology (Fig. 266): Based
on descriptions of reproduction in population
from the Gulf of Aqaba, Red Sea (Hughes
& Lewis, 1974) and Moorea, South Pacific (Phillips & Shima, 2010; Phillips, 2011): 1-58 stalked egg capsules at different stages of development per female; each capsule containing 73-571 eggs; to 4 mm long.

Hatchlings actively swim, feed on planktonic algae (planktotrophic), surviving for several weeks before metamorphosing in response to settlement cues from coralline algae. The sex ratio is biased towards females with increasing body size, suggesting protandric hermaphroditism. Adults live in areas with high wave activity (Yonge, 1932; Hughes & Lewis, 1974); solitary but often found in great abundances of 22 m-2 in the Red Sea and up to 520 m2 in Guam (Smalley, 1984).

68 GOLDING ET AL.

Comparative Remarks

Distinguished from C. robinsoncrusoei n.
sp. by its much larger size, deeply concave operculum, complex protoconch sculpture and planktotrophic larval biology. Several other
vermetids belonging to Thylacodes (formerly Serpulorbis) grow to a similar size to C. maxi-mum, but lack an operculum and could not be confused if the animal is observed.

Taxonomic Remarks

The anatomy of the specimens examined during the present study generally agrees with earlier accounts that focused on the feed-ing Strategies (and associated structures) of “Dendropoma maximum” (Yonge, 1932; Mor-ton, 1965). One point of difference is that the mantle of female specimens examined herein was divided to accommodate the attachment of stalked egg capsules to the shell wall (see also Phillips & Shima, 2010), whereas Yonge (1932) did not record this character (although the condition of the mantle margin was not specified), and Morton (1965) stated that the female mantle was entire. It is unclear whether this inconsistency represents genuine varia-tion within the species, or is due to incomplete knowledge of the morphological and systematic diversity within Dendropoma s.l.
Specimens collected from the southern and central Pacific Ocean were used to describe the anatomy and larval biology of C. maximum. By contrast, our molecular data come from the extreme western end ofthe range (Jordan). The capacity for planktotrophic larval dispersal in C. maximum supports the hypothesis that it is a single taxon by facilitating medium- to long-range genetic mixing. On the other hand, descriptions of living animals range from feeding exclusively by ciliary currents (e.g., Yonge, 1932; as Verme-tus novaehollandiae) to feeding by conspicuous mucous net (e.g., Kappner et al., 2000). It will be necessary to examine further wet-preserved material from across the entire range to confirm that this species is cohesive across its range.

Distribution (Fig. 251)

Tropical Indo-Pacific, from the east Pacific Ocean to the Red Sea. Recorded in the litera-ture from various locations including: the Gulf of Aqaba (Kappner, 1998), Indonesia (Scaps & Denis, 2008), the Great Barrier Reef (Yonge, 1932), Pitcairn Islands (Irving, 1995) and the Cocos-Keeling Islands (Maes, 1967).

Ceraesignum robinsoncrusoei п. sp.

Dendropoma “Chile” — Rawlings et al., 2001: 1605 [sequence and gene arrangement data].

Type Locality

Rocky reef at NE point of Cumberland Bay, near Punta Pangal; Robinson Crusoe Island (Isla Robinson Crusoe), Juan Fernandez Archi-pelago, Chile: ca. 33.641°S, 78.823°W [Islas Océanicas de Chile 1997 Expedition sta. IOC 97-57; ВЛ Carlos Porter).

Material Examined

Juan Fernändez Archipelago, Chile: All from station IOC-57 (single collecting event, coll. R. Bieler by SCUBA, March 7, 1997, 3-5 m): Holotype: MNHNC 5988 ex FMNH 329353, 329354, 70% EtOH (one cluster with several attached paratypes , MNHNC 5989; Figs. 282, 283). Paratypes: FMNH 326906, 70% EtOH (many specimens), Bouin’s fluid (13 specimens), 100% EtOH (8 specimens), dry (shell fragments) [DNA sequence data].

Etymology

Named after Robinson Crusoe; this fictional character from Daniel Defoe’s 1719 novel is the namesake of the type locality (Isla Robinson Crusoe). Defoe’s story was inspired by the travails of Scottish sailor Alexander Selkirk who was rescued from this island in 1708. Noun in genitive case.

Description

Teleoconch (Figs. 267-269): Apertural diam-eter to 4.5 mm; shell length to 15 mm; diam-eter of last whorl to 10 mm. Up to six partially or entirely overlapping whorls coiled initially in concentric spiral, straightening towards aperture. Exterior surface matte, white with brown patches showing through from interior surface; sculpture of irregular transverse lamellae. Interior surface white to pale fawn with brown patches.

Protoconch (Figs. 270-272): Settled proto-conchs diameter to 700 um, height to 710 um. “Hook” projection strong. Globular, with large increase in whorl size; moderately deep suture; 1.25 whorls; sculpture absent. Color-less or pale brown.

“DENDROPOMA GROUP” WORM-SNAILS 69

Operculum (Figs. 273, 274): Diameter to 2.3 mm, filling about 80-90% of apertural tube diameter. Shaped like shallow, concave sau-cer. “Fingerprint” texture on muscle attach-ment area composed of low, widely-spaced, concentric ridges.

Radula (Fig. 275): Colorless. Length of ribbon 1.3-2.1 mm, width 220-250 um, 32-49 rows. Lateral tooth: two cusps on inner side, 2-3 cusps on outer side. Inner marginal tooth: 1 cusp on inner side, 2-3 cusps on outer side.

narrow food groove present. Body color of living animal velvety black; with orange band under the transparent rim ofthe mantle margin; pedal tentacles black, tips of cephalic tentacles lacking pigment; pedal disk around operculum with iridescent green sheen; outer part of operculum appearing lighter-colored from white pigment underneath; forehead be-tween cephalic tentacles with white pigment band. Color of specimens preserved in 70% EtOH: head/foot pale grey; sole of foot, lips, dorsal surface of head and neck dark grey; black speckles radiating from mouth; parallel stripes of black pigment on lateral (including
surface of tentacles) and lower surfaces of
snout; edge of mantle pale grey fading to

External Morphology and Color (Figs. 276,
277): Body length to 28 mm. Head rounded,
large compared to foot muscle; shallow,

FIGS. 267-275. Ceraesignum robinsoncrusoei n. sp., Robinson Crusoe Island, Chile. FIG. 267: Cluster of specimens encrusted with coralline algae. Holotype (asterisk) and paratypes, MNHNC 5988, 5989. Scale bar = 20 mm; FIG. 268: Holotype specimen (asterisk). Holotype on right. Scale bar = 10 mm; FIGS. 269-275: Paratypes, FMNH 326906. FIG. 269: SEM image of teleoconch sculpture. Scale bar = 200 um; FIGS. 270-272: Intracapsular larval shells. Scale bars = 100 um. FIG. 270: Apertural view; FIG. 271: Abapertural view; FIG. 272: Apical view; FIGS. 273, 274: Operculum. Scale bar = 300 um. FIG. 273: Interior surface; FIG. 274: Detail of muscle attachment area on interior surface; FIG. 275: Central section of radula. Scale bar = 50 um.

70 GOLDING ET AL.

u
SK ES Er

NÓEN R,

FIGS. 276-280. Anatomy of Ceraesignum robinsoncrusoein. sp. Paratypes, FMNH 326906, Robinson Crusoe Island, Chile. FIG. 276: Body of a female brooding egg capsules. Scale bar = 2 mm; FIG. 277: Head and mantle margin of an immature specimen. Scale bar = 1 mm; FIG. 278: Mantle cavity of a brooding female. Scale bar = 2 mm; FIG. 279: Pallial oviduct. Scale bar = 1 mm; FIG. 280: Stalked egg capsules containing embryos at early and late stages of development. Scale bar = 1 mm.

white; digestive gland pale brown with dark
brown speckles.

Development and Ecology (Fig. 280): three
stalked egg capsules per female; 20-35 em-
bryos per capsule; up to 600 um diameter; de-
Pallial and Reproductive Anatomy (Figs. 278, velopmental stages in single female spanning 279): Gill 0.2x mantle width; gill leaflets
triangular, short, breadth equal to height;
16 leaflets per mm. Osphradium 1.5 mm
long; margins smooth. Fecal pellets ovoid.
Hypobranchial gland pale brown, covering
most of pallial oviduct. Brooding females with mantle slit.

from cleaving eggs to pediveligers. Details of larval biology not known, but intracapsular larval shells same size as settled protoconchs removed from substratum around adults, sug-gesting direct development. Adults living in close proximity to each other, forming crusts on volcanic rock ledges and living bivalve

“DENDROPOMA GROUP” WORM-SNAILS 71

(Chama) specimens. Probably protandric hermaphrodite judged by prevalence of fe-males among large specimens.

Comparative Remarks

Molecular and morphological evidence sup-ports a close relationship with only one other species (C. maximum). Ceraesignum robin-soncrusoei n. sp. can be separated from C. maximum by its much smaller size, concentric spiral rather than irregular shell growth, unsculp-tured protoconch, flatter operculum, and differ-ent reproductive strategies. Another species of operculate vermetid, Dendropoma mejillonense, was recently described from northern mainland Chile (Pacheco 8 Laudien, 2008). These two Chilean species are easily distinguished by their opercula, shells and reproductive biology, for example D. mejillonense broods its unstalked egg capsules in the mantle cavity and produces distinctively sculptured protoconchs.

Distribution (Fig. 251)

Known only from the type locality at Robinson Crusoe Island in the Juan Fernández Island chain, Chile. The type locality is 160 km from suitable habitat at Alexander Selkirk Island, and 770 km south of the Desventuradas Islands. Despite intensive scuba sampling during the IOC-97 Expedition (resulting in collections of other vermetid species), C. robinsoncrusoei п. sp. was not found on Alexander Selkirk Island or the Desventuradas islands and is not re-corded from mainland Chile. This species might be endemic to Robinson Crusoe Island.

Cupolaconcha n. gen.

Dendropoma sensu Hadfield et al., 1972: 81— 98 (in part); Safriel & Hadfield, 1988: 1-13; Gardner, 1989: 250-254. Non Dendropoma Mörch, 1861.

Type Species

Dendropoma meroclistum Hadfield & Kay in Hadfield et al., 1972 [as D. meroclista].

Etymology

From the distinctive domed aperture of the shell that characterizes the genus. Composed of the architectural term “cupola”, describing a domed roof, and the Latin concha for molluscan shell. Noun of feminine gender.

Diagnostic Description

Teleoconch: Small (maximum dimension 6.5— 14.5 mm), “tube” narrow (apertural diameter excluding dome 1.2—2.5 mm). Tightly-coiled, irregular *Turritella-squeezed-sideways” growth form with 5-8 partially or entirely over-lapping whorls cemented to, or entrenched in, surface of substratum (shell, rock or coral); aperture often raised above substratum to form a feeding tube; encrusted with calcare-ous algae except for area around aperture; scars from earlier feeding tubes present. Shell thin; aperture covered by delicate, convex dome with elliptical to lens-shaped slit at apex. Color and sculpture of exterior surface vari-able. Interior surface color variable; smooth except for crowded, posteriorly-directed den-ticles covering columellar surface; concave septa present occasionally in early whorls.

Protoconch: Settled protoconch diameter 310- 530 um, height 320-420 um. Strong “hook” projection present on apertural lip. Biphasic growth evident in some taxa; protoconch shape variable; 1.3—2.5 whorls; sculpture ab-sent or presentas spiral pustules or threads; spiral keel(s) at base of whorl absent or pres-ent. Colorless or brown, transparent.

Operculum: Slightly oval (subcircular) in axial profile; diameter proportional to shell size, 600-1,100 um. Composed of two layers; inte-rior layer (attached to surface of foot) delicate, transparent, brown, chitinous disc overlaid by exterior layer of white calcareous substance forming dome-shaped deposit with irregular structure and texture. Margins of chitinous layer protruding from beneath calcareous deposit, rolled towards foot. Interior surface smooth except for slightly convex muscle at-tachment area on (embedded in foot muscle) with lightly pitted texture.

Radula: Taenioglossate, transparent, color-less. Length of ribbon 350-1,000 um, width 70-145 um; 22-42 rows (proportional to shell size). Trapezoidal rachidian tooth with prominent central cusp flanked on each side by 3-4 smaller cusps decreasing in size outwardly. Base of lateral tooth notched to interlock with rachidian and inner marginal teeth; elongate main cusp flanked by variable number of cusps on inner and outer sides. Inner marginal tooth slender with variable number of cusps on inner and outer sides. Outer marginal tooth smooth on outer side,

12 GOLDING ET AL.

variable number of splayed, digitiform cusps
present on inner side; base with prominent semicircular or triangular projection.

External Morphology and Color. Body of animal
slender (length 18-24 mm in examined wet
material), occupying 4-5 whorls of shell; three earliest whorls composed of gonad and diges-tive gland. Columellar muscle continuing for ~2 whorls. Pedal tentacles short (in preserved specimens). Head slightly bulbous; cephalic tentacles short (in preserved specimens), broad, with slightly protruding ommatophore bearing eye at outer base; right side of head with broad food groove. Adult female mantle divided by pallial slit varying from shallow notch to deep incision running for half mantle length (brooding females), slightly left of mid-line. External body coloration variable.

Pallial and Reproductive Anatomy: Gill quarter mantle width, full length of mantle cavity; gill leaflets triangular, breadth greater than height; ~20—30 leaflets per mm. Osphradium short and narrow, 600-800 um long, margins irregular; anterior tip curled towards columel-lar muscle. Rectum running from coelom to anterior right edge of mantle opening, without deviations or kinks; fecal pellets spherical to elongate. Hypobranchial gland transparent brown, covering mantle surface between gill and rectum, sometimes also partially cover-ing rectum, greatly developed in brooding females. Pallial oviduct triangular, dimen-sions variable; proximal, large, glandular diverticulum present, fused to mantle roof. Single spherical seminal receptacle bulb (containing sperm) with short duct present, embedded in ventral glandular lining of pal-lial oviduct, pointing away from open groove. Male reproductive system unknown.

Development and Ecology: Up to six stalked egg capsules attached to shell wall in single row corresponding to position of mantle slit in females; double-walled capsules semi-transparent, spherical to ovoid, diameter increasing with development of embryos, -600-1,300 um; color and number of eggs/ embryos per capsule varying between spe-cies. Larval biology varying between species. Adults either solitary or gregarious.

Comparative Remarks

Two previously-described species in this group were placed in Dendropoma, but are readily

distinguished by several major morphological characters. The most conspicuous synapomor-phy of Cupolaconcha n. gen. is the presence of a calcareous layer on the outer surface of the flat, chitinous operculum. This structure is not found in any other vermetid. Observations of the living animal by M. G. Hadfield (personal communication, 2011) indicate that the calcar-eous deposit is gradually formed in thin layers by repeatedly “swiping” the foot and operculum inside the mantle margin. This incremental process may explain the irregular and variable structure of the calcareous layer, which when fully developed fits neatly into the shell dome. The shell of Cupolaconcha is more elongate and the center of each successive whorl is displaced further sideways than the typical shorter and more-or-less concentric spiral shells typical of Dendropoma. The aperture is strikingly different from the typical vermetid (and gastropod) form due to the presence of a dome of shell restricting the aperture to an oval or lens-shaped hole at its apex. The anatomy of Cupolaconcha differs from the traditional concept of Dendropoma by the presence of a mantle slit in females (asso-ciated with the attachment of egg capsules to the interior wall of the shell), a character found in other vermetid genera such as Thylacodes (formerly Serpulorbis), Vermetus, and most species of Petaloconchus. However, this study has revealed that Dendropoma s.l. comprises several morphologically and genetically distinct groups, some of which share this feature.

Taxonomic Remarks

The description of the proposed type species, C. meroclista (Hadfield et al., 1972), acknowl-edged some discrepancies between “Dendropo-ma” meroclista and other Dendropoma species, but did not advocate generic separation. Gardner (1989), in describing a related species from the Pacific coast of Mexico (C. krypta), suggested that in future both species should be moved to a distinct subgenus within Dendropoma or to a new genus, pending a revision of Dendropoma. Molecular data presented here (see Phylogeny section) strongly support the reciprocal mono-phyly of Cupolaconcha n. gen. (including the type species C. meroclista) and the group comprising of the remainder of Dendropoma s.l. Cupolacon-cha n. gen. occupies a different section of the vermetid tree than Dendropoma, and is more closely related to Petaloconchus.
With the benefit of a molecular phylogeny, comprehensive anatomical information, and the discovery of additional diversity, Cupolaconcha

“DENDROPOMA GROUP” WORM-SNAILS 73

FIG. 281. Distribution map of Cupolaconcha n. gen. based on material examined in this study. Filled diamond = C. guana n. sp.; hollow diamond = C. meroclista; filled square = C. sinaiensis n. sp.; hol-low square = C. krypta; filled triangle = C. maldivensis n. sp.; hollow triangle = Cupolaconcha sp. (undescribed species included in molecular phylogeny).

n. gen. can be recognized as a distinct genus
not closely related to Dendropoma s.s.

Diversity and Distribution (Fig. 281)

Two previously-named species are included
in Cupolaconcha n. gen. Below, we present three new congeneric taxa. The distribution of this group is now known to extend across the tropical Pacific and Indian Oceans and also includes the Red Sea, west coast of Mexico and Caribbean. Cupolaconcha п. gen. is not known from the non-Caribbean Atlantic Ocean or from any temperate areas. The animals are found cemented to rock, shell, and coral substratum (Hadfield et al., 1972) in the intertidal to subtidal zone and are known in some areas to form biogenic reefs (Safriel & Hadfield, 1988). This study is based on a limited number of samples from few locations. The high diversity observed may perhaps be attributed to the combined effects of geographic isolation and (probably) direct development in most species. In the molecular phylogeny, a single specimen of an unknown Cupolaconcha species col-lected at Rapa Iti Island in French Polynesia was found to be sister to, but distinct from, the sequences obtained from a single Hawaiian

specimen of C. meroclista. This indicates that there is at least one additional undescribed taxon in this species complex. We predict that many more species of Cupolaconcha n. gen. will be found in areas where the worm-snail fauna has not been adequately studied.

Cupolaconcha meroclista
(Hadfield & Kay, 1972)
n. comb.

Dendropoma meroclista [sic] Hadfield & Kay in Hadfield et al., 1972: 83-84, figs. 3, 4, 19F; Kay, 1979: 104, fig. 39A; Safriel & Hadfield, 1988 (in part): 1-13, figs. 2A, 3, 4A; Bieler & Petit, 2011: 46.

Type Locality

Coralline algal-encrusted reef, Mokuoloe Island (Coconut Island), Kaneohe Bay, Oahu, Hawaii, U.S.A.: 157.7861°W, 21.4361°N.

Material Examined

Holotype: BPBM 8931.
Hawaiian Islands, U.S.A.: FMNH 329347: Ho-nolulu; coll. К. Bieler, 70% EtOH (1 specimen

74

attached to shell of Eualetes tulipa); FMNH 329348: shallow water, old reef flat, Kaneohe Bay, Oahu, approx. 21.43°N, 157.79°W, coll. R. Bieler, December 1986, 70% EtOH (many); FMNH 329349: 0.1 m at low tide, beach rock on reef flats, Diamond Head Beach, Oahu, ap-prox. 21.43°N, 157.79°W, coll. R. Bieler, March 28, 1988, 70% EtOH (many); FMNH 328505: Kaneohe Bay, Oahu, 21.436°N, 157.791°W, coll. M. Hadfield, 1998, 95% EtOH (many, bodies only) [DNA sequence data].
Guam: UF341500: Pago Bay, Mariana Islands, 13.42°N, 144.78°E, coll. W. Kelly, June 29, 2003, 95% EtOH (whole body and shell), [DNA sequence data].
Australia: AM C.407574: 0.3 m, near shore in lagoon off E end of Heron Island, Capricorn Group, Great Barrier Reef, QLD, Australia, 2343375, 151.95°Е colli W. FrPoöhger, De-cember 24, 1976, 5% SW formalin (many); FMNH 327031: 10 m, on underside of dead coral slab, with other vermetids (Petalocon-chus and Thylacodes spp.), S end of Long Island, Gros Island Channel, Houtman Abrol-hos, WA, coll. R. Bieler, F. Wells & C. Bryce, May 23, 1994; 70% EtOH (1 specimen). Papua New Guinea: AM C.407569: on fringing reef and in lagoon of reef just S of Magulata Pt., NW Kiriwina Island, Trobriand Group, 8.455; 19 1E, coll. Wor Pender & Р.Н. Colman, June 5, 1976, 5% SW formalin (one specimen attached to shell of Strombus sp.).

Description

Teleoconch (Figs. 282-287): Hawaiian and Heron Island populations: apertural diameter to 1.6 mm; shell length to 5.6 mm; diameter of last whorl to 3.7 mm. New Guinea speci-men: apertural diameter 2.5 mm; shell length 14.5 mm; diameter of last whorl 3.7 mm. Up to 6 partially or entirely overlapping whorls cemented to, but not deeply entrenched in, substratum; aperture occasionally rising ~1 mm above substratum as short feeding tube; scars from abandoned feeding tubes rarely present. Exterior surface glossy, honey brown to dark purple, semi-transparent around aperture; sculpture of undulating, irregularly-spaced, bulging, transverse folds. Interior sur-face dark brown to white, sometimes stained green (Hadfield et al., 1972).

Protoconch (Figs. 288-290): Hatchlings and settled protoconch diameter 360 um [450 um according to Hadfield et al. (1972)], height 360 um. No evidence of biphasic growth;

GOLDING ET AL.

globular with small increase in whorl size, shallow suture; 1.3 whorls; sculpture absent on first whorl, sculpture of either variably-developed pustulose sculpture (Hawaiian population) increasing in density towards lip, arranged into 9-15 distinct spiral bands positioned below shoulder, or lacking sculp-ture entirely (Heron Island, Great Barrier Reef population); single weak spiral keel in lower quarter of whorl present in most specimens from Hawaii. Colorless to very pale brown.

Operculum (Figs. 291-293): Slightly oval in axial profile; diameter to 1,000 um. Exterior surface of calcareous deposit pitted, irregular but often with coarse, jagged concavity at apex of dome or off-center.

Radula (Fig. 294): Length of ribbon 600-950 um, width 80-145 um; 30-42 rows. Lateral tooth: two cusps on inner side, 2-4 cusps on outer side. Inner marginal tooth: 2 cusps on inner side, 3-5 cusps on outer side. Outer marginal tooth: two cusps on inner side; base with prominent semicircular projection.

External Morphology and Color (Figs. 295, 296): Body length to 24 mm. Head-foot, tentacles described by Hadfield et al. (1972) as “dark purple or black with a few superficial markings”; specimens preserved in 5% SW formalin and 70% EtOH entirely devoid of pig-mentation except for dorsal surface of head bearing “mosaic” pattern of brown pigment superimposed with white spots; digestive gland olive green with dark brown speckles; ovary pale orange; testis not observed. Liv-ing Western Australian specimen (FMNH 327031) flesh-colored, with dark brown patches on foot; mantle margin with red surface pigment and flesh-colored edge with embedded white granular clusters; cephalic and pedal tentacles translucent flesh-colored with few white spots (thus indicating intraspe-cific variability in coloration or additional unrecognized species diversity).

Pallial and Reproductive Anatomy (Figs. 297, 298): Pallial oviduct narrow; 2.3 mm long, 400 um wide. Proximal diverticulum curved towards coelomic oviduct, constricted near junction with pallial oviduct.

Development and Ecology (Fig. 299): Stalked egg capsules found in one living and two preserved female specimens: four capsules at different stages of development per female

“DENDROPOMA GROUP” WORM-SNAILS 7

[up to six capsules may occur (Hadfield et al., 1972)]; each capsule containing 4-12 eggs/embryos; eggs/embryos dark yellow when preserved in 70% EtOH. Larval biol-ogy not observed, but reported by Hadfield

et al. (1972) and Safriel & Hadfield (1988) as
direct developing, with crawl-away hatchlings
and possibly occasional planktonic larvae.
Taylor (1975: 76) hypothesized the veligers
as probably “not planktonic for more than a

FIGS. 282-294. Cupolaconcha meroclista (Hadfield & Kay, 1972). FIG. 282: Specimen partly encrusted with coralline algae. Scale bar = 1 mm; FIG. 283: Coral with many specimens attached. AM C.407574, Heron Island, Australia. Scale bar = 5 mm; FIG. 284: Large specimen cemented to shell of Strombus sp. (coralline algae partially removed). AM C.407569, Papua New Guinea. Scale bar =2 mm; FIG. 285: SEM image of domed aperture and (broken) elliptical slit. Scale bar = 500 um; FIG. 286: Sculpture on teleoconch. Scale bar = 100 um; FIG. 287: Sculpture on columellar surface of shell interior. Scale bar = 50 um; FIGS. 288-290: SEM images of intracapsular larval shells. Scale bars = 100 um. FIG. 288: Apertural view; FIG. 289: Abapertural view; FIG. 290: Sculpture near aperture; FIGS. 291-293: SEM images of operculum. Scale bars = 100 um. FIG. 291: Exterior surface. AM C.407574, Heron Island, Australia; FIG. 292: Interior surface; FIG. 293: Lateral and oblique lateral views of calcareous layer (chitinous layer removed); FIG. 294: Central section of radula. Scale bar = 50 um. FIGS. 282, 285-290, 292-294: FMNH 329349, Oahu, Hawaii.

76 GOLDING ET AL.

FIGS. 295-299. Anatomy of Cupolaconcha meroclista (Hadfield & Kay, 1972). FIG. 295: Body of a female brooding egg capsules. Scale bar = 1 mm; FIG. 296: Head-foot and notched anterior mantle margin of female without egg capsules. FMNH 329347, Hawaii. Scale bar = 500 um; FIG. 297: Mantle cavity of a brooding female. Scale bar = 1 mm; FIG. 298: Pallial oviduct. Scale bar = 200 um; FIG. 299: Stalked egg capsules at early and late stages of development. Scale bar = 200 um. FIGS. 310, 312-314: FMNH 329349, Oahu, Hawaii.

few hours, or at most, a few days.” Adults
generally solitary, but sometimes settling
within 1-2 mm of each other or with other
vermetids such as Dendropoma gregarium;
common in intertidal reef zone attached to rocks and coral (Hadfield et al., 1972).

Comparative Remarks

Shell darker and more purplish than other species of Cupolaconcha n. gen.; larger than other species except C. guana n. sp. Proto-conch sculpture variable but pustulose when

present and never condensing to form spiral threads as in C. krypta; single spiral keel weak. Pigment on head-foot dark purple to black with white markings in life. Egg capsules containing up to six eggs/embryos.

Taxonomic Remarks

Although the anatomy and shell morphol-ogy of specimens from the type locality has been described in detail here, there are some discrepancies with outlying populations in Aus-tralia and Papua New Guinea. In relation to the

“DENDROPOMA GROUP” WORM-SNAILS DR

Hawaiian specimens, the shells of specimens from Papua New Guinea are larger and those from Heron Island are smaller. In addition, protoconchs from Heron Island are uniformly without sculpture. Protoconch sculpture was variable between specimens from Hawaii, and some had greatly reduced sculpture, suggesting that this character varies between individuals. These differences were less than those observed between the other species in Cupolaconcha, so we have tentatively assigned the non-Hawaiian material to C. meroclista. Faucci (2007) identified four major clades of Cupolaconcha meroclista in her phylogeo-graphic analysis of 72 specimens from the Hawaiian archipelago and surrounding Pacific islands. Nucleotide sequence of CO/ from our samples from Kaneohe Bay, Oahu, was identi-cal to her “Haplotype 14” nested in the major clade of specimens sampled from across the Pacific, and including the type locality of this taxon. The existence of three other strongly supported and genetically divergent clades of vermetids with the same general appearance as C. meroclista, one including specimens from the Hawaiian Islands, suggests that cryptic species are currently residing under this taxon name (Faucci, 2007).
The species epithet was explained by Had-field & Kay (1972: 84) as “derived from the Greek, meaning partly closed.” The Greek kleistos (“closed”) was Latinized to clistus-a-um, a Latin adjective, and combined with the Greek adverbial meros (“partially”). As an adjective, it takes the gender of the genus, and when combined with (neuter) Dendropoma, it should have been Dendropoma meroclistum.

Distribution (Fig. 281)

Material from Hawaii (including the type local-ity), the Marshall Islands (Hadfield et al., 1972), Heron Island on the Australian Great Barrier Reef (this study) and Papua New Guinea (this study) are here referred to C. meroclista. The species is known from several remote island and mainland locations throughout the tropical central and western Pacific Ocean, but has not been recorded from many areas within its presumed distribution, perhaps due to its inconspicuous appearance. “Dendropoma” meroclista has been recorded by Kelly (2007; fig. 9c) from Guam and by Fukuda (1993) from the Ogasawara Islands in Japan, but the true identity of material from those locations requires confirmation in light of the additional diversity described here.

Cupolaconcha krypta
(Gardner, 1989)
n. comb.

Dendropoma krypta [sic] Gardner, 1989: 250— 254, figs. 1-4; Bieler & Petit, 2011: 43.

Type Locality

Isla Isabela, Nayarit, Mexico (Pacific Ocean): 21.85°N, 105.92°W.

Material Examined

Paratypes: CASIZ 065116: attached to large limpet shell from type locality, coll. G. D.H anna & E. K. Jordan, CAS expedition ca. 1925, dry (many shells, some with dried animals).

Description

Teleoconch (Figs. 300-304): Apertural diam-eter to 1.2 mm; shell length to 6.8 mm; diam-eter of last whorl to 3.5 mm. Up to six partially or entirely overlapping whorls cemented to, but not deeply entrenched in, substratum; aperture occasionally raised ~1 mm above substratum as short feeding tube; scars from abandoned feeding tubes rarely present. Ex-terior surface matt, pale tan to pinkish brown. (not honey brown as described by Gardner, 1989), semi-transparent around aperture; sculpture of undulating, irregularly-spaced, bulging, transverse folds. Interior surface pale brown.

Protoconch (Fig. 305): Settled protoconch diameter 350 um, height 320 um. No evi-dence of biphasic growth; globular with small increase in whorl size, moderately deep suture; 1.5 whorls; sculpture absent on first whorl, sculpture of many (> 30) pustulose to thread-like spiral bands developing towards lip; single spiral keel present in most speci-mens. Pale brown.

Operculum (Figs. 306, 307): Slightly oval in axial profile; diameter to 600 um. Exterior surface of calcareous deposit slightly granu-lar, lacking concavity. Interior surface as for genus, not observed to form a distinct plug as described by Gardner (1989).

Radula (Fig. 308): Length of radula ribbon 660 um, width 100 um; 27 rows. Lateral tooth: 2-3 cusps on inner side, 2-3 cusps on outer side. Inner marginal tooth: 2-3 cusps on inner

78 GOLDING ET AL.

side, 2-3 cusps on outer side. Outer marginal
tooth: 2-3 cusps on inner side; base with
prominent semicircular projection.

External Morphology and Color (Fig. 309):
Anterior body of animal known only from 3
rehydrated partial specimens removed from dry paratype lot, confirming some generic features and the following details of pigmen-tation: head-foot pale brown, with blackish brown pigment covering dorsal surface and sides of head, including most of snout, sur-

rounded posteriorly and laterally by “mosaic” pattern of brown pigment superimposed with white spots; cephalic tentacles and lips white; Sparse brown pigment on lateral surfaces of foot and opercular lobe.

Pallial and Reproductive Anatomy: Not known.

Development and Ecology: Egg capsules not
known. Adults gregarious, forming a dense,
monospecific crust covering the surface of a
large limpet (paratypes).

FIGS. 300-309. Cupolaconcha krypta. Paratypes, CASIZ 065116, Isla Isabela, Mexico. FIG. 300: Speci-mens attached to a large limpet shell, only apertures are visible beneath encrusting epifauna. Scale bar = 10 mm; FIG. 301: Partly excavated shells. Scale bar = 2 mm; FIG. 302: Domed apertures with elliptical slits. Scale bar = 1 mm; FIG. 303: SEM image of teleoconch sculpture. Scale bar = 100 um; FIG. 304: Sculpture on columellar surface of shell interior. Scale bar = 100 um; FIG. 305: Abapertural view of protoconch. Scale bar = 100 um; FIGS. 306, 307: SEM images of operculum. Scale bar = 100 um. FIG. 306: Exterior surface; FIG. 307: Interior surface; FIG. 308: Central section of radula. Scale bar = 20 um; FIG. 309: Head-foot (without operculum) of a rehydrated specimen. Scale bar = 200 um.

“DENDROPOMA GROUP” WORM-SNAILS TS

Taxonomic Remarks

The Greek word krypte was properly Latinized to krypta by the original author, who chose to maintain the spelling with a “К” and explained “from the Greek, meaning hidden, covered, concealed.” The resulting adjectival form kryptus-a-um should have been used as kryptum in the original combination with (neuter) Dendropoma.

Comparative Remarks

Shell paler and smaller than C. meroclista and C. guana n. sp. Protoconch similar to that of C. meroclista but spiral bands of pustules condense to form threads near aperture; spiral keel also more strongly developed.

Distribution (Fig. 281)

Cupolaconcha krypta is known only from a single collecting event at Isla Isabela in Mexico. The animals are extremely cryptic because of their minute size and growth under a thick layer of encrustation, and likely are present at other nearby sites on the east Pacific Rim.

Cupolaconcha guana n. sp.

Vermetus conicus “Dillwyn and Wood” var. a personata juv. Mórch, 1862: 341-342 [infra-subspecific]; Bieler & Petit, 2011: 52. Non Serpula conica Dillwyn, 1817.

Type Locality

5-10 m depth, cove at Iguana Head at SW point of Guana Island: 18.474°N, 64.582°W.

Material Examined

Original material of Vermetus conicus var. personata of Mórch (1862) from St. Croix, U.S. Virgin Islands (ZMC).
British Virgin Islands: Holotype: FMNH 329350: coll. R. Biele&rT . M. Collins, August 9, 2010, 70% EtOH. Paratypes: FMNH 326719: with holotype, 70% EtOH (9 specimens); FMNH 326713: SE part of White Bay, near Monkey Point, Guana Island, British Virgin Islands, 5-6 m depth, 18.446°N, 64.572°W, coll. R. Bieler & T. M. Collins, August 8, 2010, 70% EtOH (10 specimens). FMNH 326700: 2 m, patch reefs, White Bay, Guana Island, 18.471°N, 64.574°W, coll. R. Bieler & T. M. Collins, August 5, 2010, dry, 70% EtOH (20 specimens) [DNA sequence data].

U.S. Virgin Islands: FMNH 328509: 10-15 m depth, Long Reef $ of Christansted, St. Croix, coll. К. Bieler &М . Ogden, February 28, 1987, 70% EtOH (3 specimens).
Belize: FMNH 326930: Carrie Bow Cay, Stann Creek District, 16.803°N, 88.082°W, coll. R. Bieler, March 1986, 70% EtOH (1 animal) and dry (2 shells). FMNH 326932: Carrie Bow Cay, Stann Creek District, 16.803°N, 88.082°W, coll. R. Bieler, March 1986, dry (many, attached to coral substratum); FMNH 327154: attached to coral heads and algae-encrusted coral rubble on shallow subtidal reef, 1-2 m, Little Cat Cay, Stann Creek District, 16.151°N, 88.200°W, coll. R. Bieler, T. Collins, R. E. Golding, T. Rawlings & P. Sierwald, April 17, 2011, RNAlater (8 tissue samples), 95% EtOH (12 animals), 5% SW formalin (many attached to chunks of substratum) [DNA sequence data]; FMNH 327196: Carrie Bow Cay, Stann Creek Dis-trict, 16.803°N, 88.082°W, coll. R. Bieler, April 2011, dry (many attached to dead shell); FMNH 327169: shallow subtidal coral rubble, under boulders, lagoon E of Carrie Bow Cay, Stann Creek District, 16.803°N, 88.082°W, 20th April 2011, RNAlater (1 animal), 95% EtOH (1 animal), dry (2 shells); FMNH 327185: coral rubble and living coral heads, lagoon E of Carrie Bow Cay, 16.803°N, 88.082°W, April 24, 2011, RNAlater (4 tis-sue fragments), 95% EtOH (3 animals), 70% EtOH (egg capsules and many specimens attached to chunks of substratum), 5% SW formalin (3 shells with animals).
Bahamas: FMNH 335076: 6-8 m, reefs NE of Great Abaco Island, 26.636°N, 77.0352°W, coll. R. Bieler & P. Sierwald, August 8, 2012, dry and ethanol (many), [DNA sequence data].
Florida, U.S.A.: FMNH 326731: Looe Key reef, Florida Keys, 24.4110°N, 81.4091°W, coll. R. Bieler, September 9, 2011, RNAlater (2 tissue samples), 95% EtOH (2 bodies), dry (2 shells); FMNH 327227: on gorgonians and Dendostrea frons, Missouri Key, 24.674°N, 81.238°W, coll. R. Bieler & P. Sierwald, Sep-tember 2011, dry (many); FMNH 328503: small island oceanside of Bahia Honda Bridge, Florida Keys, 24.6479°N, 81.2842°W, coll. R. Bieler & P. Sierwald, April 9, 2012, dry (many, on lobster trap parts).

Etymology

From the type locality on Guana Island, Brit-ish Virgin Islands. Noun in apposition.

80 GOLDING ET AL.

Description deeply entrenched in, substratum; aperture
occasionally raised -1 mm above substratum
Teleoconch (Figs. 310-315): Apertural diameter as short feeding tube; scars from abandoned
to 2.2 mm; shell length to 7.5 mm; diameter feeding tubes occasionally present. External
of last whorl to 4.5 mm. Up to eight par- surface glossy, either bright orange or dark
tially overlapping whorls cemented to, but not brown without intergrade colors, opaque;

314

FIGS. 310-321. Cupolaconcha guana n. sp. FIGS. 310, 311. Dark brown morph. FIG. 310: Holotype, FMNH 329350. Shell cleaned of encrustation. Guana, British Virgin Islands. Scale bar =2 mm; FIG. 311: Aperture with living animal. Paratype, FMNH 327154, Little Cat Cay, Belize. Scale bar = 1 mm; FIGS. 312, 313. Orange morph. FIG. 312: Paratype FMNH 326719. Scale bar = 2 mm; FIG. 313: Aperture with living animal. Paratype FMNH 327154. Scale bar = 1 mm; FIG. 314: SEM image of shell. Paratype, FMNH 326719. Scale bar = 1 mm; FIG. 315: Sculpture on columellar surface of shell interior. Paratype, FMNH 326713, Guana, British Virgin Islands. Scale bar = 100 um; FIGS. 316, 317: SEM images of intracapsular larval shells. Paratype FMNH 326719, Guana, British Virgin Islands. Scale bar = 100 um. FIG. 316: Apertural view; FIG. 317: Apical view; FIGS. 318, 319: SEM images of operculum. Paratype, FMNH 326713, Guana, British Virgin Islands. Scale bar = 200 um. FIG. 318: Exterior surface; FIG. 319: Interior surface; FIG. 320: Central section of radula. Paratype, FMNH 326713, Guana, British Virgin Islands. Scale bar = 50 um; FIG. 321: Egg capsules removed from interior shell wall. FMNH 327154. Scale bar = 500 um.

“DENDROPOMA GROUP” WORM-SNAILS 81

FIGS. 322-325. Anatomy of Cupolaconcha guana n. sp. FIG. 322: Body and mantle cavity of a female brooding egg capsules. Scale bar = 1 mm; FIG. 323: Anterior body of a female. Scale bar = 1 mm; FIG. 324: Pallial oviduct. Scale bar = 200 um; FIG. 325: Stalked egg capsules. FMNH 326713, Guana, British Virgin Islands. Scale bar = 200 um. FIGS. 322-324: FMNH 326719, Guana, British Virgin Islands.

sculpture of undulating, irregularly-spaced,
bulging, transverse folds. Interior surface
either bright orange or dark brown, matching
external shell color.

Protoconch (Figs. 316, 317): Settled proto-
conch diameter 460-530 um, height 400 um. No evidence of biphasic growth; Subplanar, with large increase in whorl size, deep suture; 1.3 whorls; sculpture absent; spiral keel ab-sent. Brown, darkest at suture.

Operculum (Figs. 318, 319): Oval in axial pro-file; diameter to 1,100 um. Exterior surface of calcareous deposit mostly smooth, some-times grainy or coarsely textured, often with concavity at apex of dome or off-center.

Radula (Fig. 320): Length of radular ribbon 340-1,000 um, width 70-135 um, 22-36

rows. Lateral tooth: two cusps on inner side, 3-6 cusps on outer side. Inner marginal tooth: two cusps on inner side, 3-4 cusps on outer side. Outer marginal tooth: 2-3 cusps on inner side; base with prominent semicircular projection.

External Morphology and Color (Figs. 311, 313, 322, 323): Body length to 18 mm. Color in life and specimens recently preserved in 70% EtOH: lateral surfaces of foot and neck dark red to rose pink; snout (except lips) and dorsal head diffuse orange-red with fine brown speckles; lips, tentacles and sole of foot cream; anterior edge of mantle brownish-red fading to cream, with dark red pigment speckles on mantle reducing in density posteriorly but especially dense in region of gill; digestive gland olive green with black flecks.

82 GOLDING ET AL.

Pallial and Reproductive Anatomy (Figs. 322,
324): Pallial oviduct broad; 1.8 mm long,
600 um wide. Proximal diverticulum straight,
not constricted near junction with pallial
oviduct.

Development and Ecology (Figs. 321, 325): Stalked egg capsules found in several pre-served and living female specimens: 2-6 capsules at different stages of development per female; each capsule containing 2-3 eggs/embryos; eggs/embryos pale, mint green in life. Hatchlings had resorbed most of the velum and were observed to crawl on the substratum, suggesting that they were not capable of planktonic dispersal. Adults soli-tary and settling mostly on exposed surfaces of dead coral in the shallow to deep subtidal. Rarely growing adjacent to conspecifics, but often concentrated in large numbers on a particular substratum.

Taxonomic Remarks

Mörch (1862: 341-342) studied specimens of this species from St. Croix and mistakenly considered them to be juveniles of a larger Caribbean species that he called Vermetus conicus [(Dillwyn, 1817)]. He (1862: 342) in-ferred that “the constricted aperture must then, of consequence, become dissolved with age.” The varietal name applied to this material by Morch, “var. a personata juv.,” is not available (see also Bieler & Petit, 2011: 6, 52).

Comparative Remarks

Shell color variable, orange morph distinct in genus; larger than other species of Cupolacon-cha п. gen. except С. meroclista. Protoconch planar, unsculptured. Head-foot pigment orange-red in life. Egg capsules containing fewer than three eggs/embryos.

Distribution (Fig. 281)

This is the only representative of Cupola-concha from the Atlantic Ocean, and is not known to occur outside the Caribbean region. Material examined in this study was collected from around the perimeter of the Caribbean Sea at Belize, the Florida Keys and the British Virgin Islands, indicating that C. guana has a widespread distribution in the region.

Cupolaconcha sinaiensis n. sp.

Dendropoma meroclista — Safriel & Hadfield, 1988 (in part): 1-13, figs. 1, 4B.
Dendropoma sp. Safriel & Hadfield, 1988 (in part): 1-13, fig. 2B, 5.

Type Locality

Gulf of Aqaba, Sinai Peninsula: approx. 29,9 N,35.0°W.

Material Examined

Israel: Holotype: FMNH 329351: coll. U. Saf-riel, pre-1987, dry (Fig. 342; 1 shell attached to substratum with paratypes). Paratypes: FMNH 328076: from type locality, coll. U. Safriel, pre-1987, dry (many specimens at-tached to substratum with holotype). FMNH 328077-328081: from type locality, coll. U. Safriel, pre-1987, dry (many specimens at-tached to chunks of substratum).

Etymology

Named for the geographic region of the type locality on the Sinai Peninsula. Adjective in genitive case.

Description

Teleoconch (Figs. 326-331): Apertural diameter to 2.3 mm; shell length to 9 mm; diameter of last whorl to 5 mm. Up to six partially over-lapping whorls deeply entrenched in substra-tum; aperture usually raised ~3 mm above substratum as moderately tall feeding tube, especially when growing in dense aggregates; remains of early feeding tubes frequently present. Exterior surface glossy, medium to dark brown, opaque; sculpture of undulating, irregularly-spaced, bulging, transverse folds. Interior surface medium brown to white.

Protoconch (Figs. 332, 333): Hatchlings and intracapsular protoconchs (initial growth phase): diameter 220 um, [~240 um accord-ing to Safriel & Hadfield (1988)], height 140 um; settled protoconchs (secondary growth phase): diameter 310 um; height 350 um [up to 400 um (Safriel & Hadfield, 1988)]. Growth divided between intracapsular and pre-settlement (planktonic?) phases with

“DENDROPOMA GROUP” WORM-SNAILS 83

transition evident in protoconch structure; hatchling protoconch almost planar, settled protoconch pupoid, sutures shallow; hatch-ling protoconch 1 whorl, settled protoconch 2.5 whorls; sculpture absent on first phase, sculpture on second phase of spiral bands of widely-spaced pustules (largest near suture) transitioning to short, oblique threads near lip; 6 spiral keels present. Honey brown.

Radula: Not observed in this study, but figured by Safriel & Hadfield (1988) showing the fol-lowing details: Width of radular ribbon 100 um. Lateral tooth: two cusps on inner side, 2-3 cusps on outer side. Inner marginal tooth: at least one cusp (partially obscured) on in-ner side, three cusps on outer side. Outer marginal tooth: two cusps on inner side; base with prominent semicircular projection.

External Morphology and Color. Not observed in this study, but described and partially figured by Safriel & Hadfield (1988) as mor-phologically identical to C. meroclista from

Operculum: Not observed in this study, but
described and figured by Safriel & Hadfield
(1988) as identical to that of C. meroclista
from Hawaii.

328.

FIGS. 326-333. Cupolaconcha sinaiensis n. sp. from the type locality at the Gulf of Aqaba, Sinai Peninsula. FIG. 326: A dense aggregate of specimens removed from rock surface. FMNH 328077. Scale bar = 5 mm; FIG. 327: Shell of holotype. FMNH 329351. Scale bar = 1 mm; FIG. 328: Broken specimen deeply entrenched into the surface of a barnacle. FMNH 328077. Scale bar = 2 mm; FIG. 329: SEM image of teleoconch sculpture. FMNH 328079. Scale bar = 200 um; FIG. 330: Sculpture on columellar surface of shell interior. FMNH 328076. Scale bar = 200 um; FIG. 331: Feeding tube with domed aperture. FMNH 328079. Scale bar = 500 um; FIG. 332: Apertural view of intracapsular larval shell. FMNH 328076; FIG. 333: Abapertural view of protoconch from recently-settled juvenile. FMNH 328079. Scale bar = 50 um.

84 GOLDING ET AL.

Hawaii with respect to the following details:
head/foot darkly pigmented, snout and tips of
cephalic tentacles pale; pedal tentacles dark
with pale spots; mantle divided by pallial slit
in females.

Pallial and Reproductive Anatomy: Not known.

Development and Ecology: Not observed in this study, but Safriel & Hadfield (1988) described developmental biology of a population from the type locality in considerable detail, not-ing in particular the following points: females brood up to six stalked egg capsules; each capsule containing 21-134 eggs (x = 65, N = 14). Larvae believed by Safriel & Hadfield (1988) to be capable of sustained plank-tonic development based on apparent shell growth between hatching and settlement (see above). Highly gregarious, forming a living crust on the intertidal seaward edge of a thick layer of dead vermetid shells cemented together (Safriel, 1966; Safriel & Hadfield, 1988).

Comparative Remarks

Most similar to C. maldivensis n. sp., in size and propensity to form a living crust of aggregated shells on substratum, but lacking crest and transverse lamellae present in C. maldivensis. Protoconch growth divided into intracapsular and (presumably) planktonic phases, resulting in unique protoconch struc-ture (2.5 whorls, pupoid shape). Egg capsules containing many more eggs/embryos (21-134) than any other species in Cupolaconchan. gen. (maximum 12).

Taxonomic Remarks

Safriel & Hadfield (1983) informally recog-nized that specimens from the type locality in the Gulf of Agaba were a distinct species from C. meroclista. They used the name “Dendro-poma sp.” in their figure legends, but did not propose a name for this taxon or offer a formal description. Here we introduce C. sinaiensis п. sp. аз a distinct species.

Distribution (Fig. 281)

The description above is based only on ma-terial from the type locality. Safriel & Hadfield (1988) reported that specimens from Madagas-car were conspecific with those from the Sinai

Peninsula, based on protoconch morphology. This remains to be tested, and at present the verified distribution is restricted to the type locality in the Gulf of Aqaba.

Cupolaconcha maldivensis n. sp.

Type Locality

Boulder zone, seaward edge of reef flat, Gan Island, Addu Atoll, Maldives: approx. 0.69°S, 73.14°E.

Material Examined

Republic of Maldives: Holotype: FMNH 329352: coll. J. D. Taylor, 1975, dry (1 shell attached to chunk of substratum with paratypes). Para-types: FMNH 328083: from the type locality, coll. J. D. Taylor, 1975, dry (many specimens with holotype); FMNH 328082: intertidal reef platform edge, Gan Island, Addu Atoll, Maldives, approx. 0.69°S, 73.14°E, coll. J. D. Taylor, 1975, dry (many).
Kenya: FMNH 328084: edge of fringing reef platform, Likoni, 4.09°S, 39.67°E, coll. J. D. Taylor, 1977, dry (many).

Etymology

Named for the geographic region of the type locality in the Maldive Islands. Adjective in genitive case.

Description

Teleoconch (Figs. 334-337): Apertural diameter to 1.5 mm; shell length to 6.5 mm; diameter of last whorl to 3 mm. Up to five widely-spaced (usually non-overlapping) whorls cemented to, but not deeply entrenched in, substratum; ар-erture usually raised ~1 mm above substratum as short feeding tube; scars from abandoned feeding tubes frequently present. Exterior surface medium to dark purplish brown, pale brown near aperture, opaque; sculpture of undulating, irregularly-spaced, bulging, trans-verse folds and scaly lamellae, with crest-like ridge running longitudinally on dorsal surface. Interior surface pale brown to white.

Protoconch (Figs. 338, 339): Settled proto-conch diameter 340-370 um, height 380 um (Maldives population) to 420 um (Kenyan population). No evidence of biphasic growth; globular with small increase in whorl size

“DENDROPOMA GROUP” WORM-SNAILS 85

(first whorl disproportionately large in Kenyan population), shallow suture; 1.5 whorls; sculp-ture absent. Honey brown.

Operculum (Figs. 340, 341): Oval in axial profile; diameter to 740 um. Exterior surface mostly smooth, sometimes grainy or coarsely textured; irregularly-shaped concavity some-times present at apex of dome or off-center.

Radula (Fig. 342): Length of radula ribbon 450-600 um, width 100 um; 25-31 rows. Lat-eral tooth: 2-3 cusps on inner side, 2-3 cusps on outer side. Inner marginal tooth: two cusps

on inner side, 4-5 cusps on outer side. Outer marginal tooth: 4-5 cusps on inner side; base with prominent triangular projection.

External Morphology and Color (Fig. 343): Anterior body of animal known only from three rehydrated partial specimens removed from dry paratype lot, showing the following features: Head-foot, snout, cephalic tentacles
and broad band on mantle margin covered
with black pigment, dorsal and lateral sur-
faces of head posterior to tentacles covered
with “mosaic” pattern of black pigment super-
imposed with white spots; lips white.

FIGS. 334-343. Cupolaconcha maldivensis n. sp. FIG. 334: Aggregate of specimens removed from rock surface. Scale bar = 5 mm; FIG. 335: Shell of holotype. FMNH 329352, Gan Island, Maldives. Scale bar = 1 mm; FIG. 336: SEM image of teleoconch sculpture. Scale bar = 200 um; FIG. 337: Sculp-ture on columellar surface of shell interior. Scale bar = 100 um; FIGS. 338, 339: Abapertural view of protoconchs from recently settled juveniles. Scale bar = 50 um. FIG. 338: Paratypes; FIG. 339: FMNH 328084, Likoni, Kenya; FIGS. 340, 341: SEM images of operculum. Scale bar = 100 um. FIG. 340: Exterior surface; FIG. 341: Interior surface; FIG. 342: Central section of radula. Scale bar = 20 um; FIG. 343: Anterior body (without calcareous layer of operculum) of a rehydrated specimen. FIGS. 334, 336-338, 340-343: Paratypes, FMNH 328083, Gan Island, Maldives.

86 GOLDING ET AL.

Pallial and Reproductive Anatomy: Not known.

Development and Ecology: Egg capsules not
known. Adults gregarious, forming a dense
colony encrusting pieces of dead coral and
rock.

Comparative Remarks

Similar to C. sinaiensis n. sp. and C. krypta in shell size, but the only species in Cupolacon-cha n. gen. that has transverse lamellae and a longitudinal crest on the exterior surface of the shell. The protoconch is globular, but lacks any distinct sculpture. Radula dentition is variable, but tends to have a greater number of cusps on the outer side of the inner marginal tooth and the inner side of the outer marginal tooth (4—5) than conspecific taxa; projection on base of outer marginal tooth triangular rather than semicircular.

Taxonomic Remarks

Material from Kenya and the Maldives was examined in the preparation of this description. Despite the considerable distance between these sites in the Indian Ocean, they appear to belong to the same species-level taxon based on morphological data. However, the Kenyan samples were in poor condition, were excluded from the paratype series, and are herein provi-sionally referred to C. maldivensis n. sp.

Distribution (Fig. 296)

Known from the Maldives in the central Indian Ocean and Kenya on the east coast of Africa.

The status of “Dendropoma” exsertum
(Dall, 1881)

This nominal species was introduced, as Bivonia exserta Dall, 1881, for a single partial shell tube collected as part of the U.S. Coast Survey at Blake Station 20, off Bahia Honda (Cuba: 23°2’30”N, 83°11’W) in ca. 400 m (220 fathoms) depth. Dall (1881: 39) remarked that it “has a remarkable structure sculpture and is only provisionally referred to Bivonia, as the operculum is unknown.” The species remained unfigured until 1889, when Dall (1889: 264, pl. 26, fig. 6) added a drawing of the holotype and referred to additional material of “Bivonia ? exserta’ from other locales from Barbados to North Carolina. He concluded that the type specimen was a juvenile shell. Dall’s species

FIGS. 344, 345. Holotype of Bivonia exserta Dall, 1881, MCZ 7445, off Bahia Honda, Cuba. FIG. 344: Attached side; FIG. 345: Free side. Scale bar = 2 mm.

was uncritically accepted in subsequent re-gional species listings, e.g., as Bivonia exserta by Maury (1922: 132) and as Dendropoma exsertum by Rosenberg (2009) and Rosenberg et al. (2009). The holotype specimen (MCZ 7445) is the apertural portion of a polychaete (Serpulidae) worm tube (Figs. 344, 345). The nominal species Bivonia exserta Dall, 1881, is here removed from the Mollusca.

DISCUSSION

Genus-Level Systematics

Previous attempts to tackle vermetid evolu-tion (Morton, 1955) and systematics have relied on characters of the adult shell alone (Carpen-ter, 1857; Mörch, 1861, 1862) or ac ombination of adult and juvenile shell morphology, growth habit, and partial accounts of the operculum (Keen, 1961). Morton (1965) reinforced and enhanced the classification introduced by Keen (1961) by including morphological descriptions of members of each genus. With each advance in our knowledge of the group, a new concept of the diversity and composition of Vermetidae has emerged. Here, we have proposed a new classification for a subset of the Vermetidae, the “Dendropoma group”, based on a greatly improved morphological dataset. Crucially, this interpretation has been supported by a new line of evidence with the construction of a molecular phylogeny. The development of a novel sys-tematic framework for these taxa provides an opportunity to examine the morphological and molecular features that define each group and

“DENDROPOMA GROUP” WORM-SNAILS 87

re-examine the evolutionary pathways leading to this diversity.
This systematic revision of Dendropoma s.l. is a substantial modification of the prevailing concept of the group, as introduced by Keen (1961) and cemented by Morton (1965). The classification presented here divides the group of taxa previously assigned to Dendropoma s.l. into four distinct genera belonging to two separate branches of Vermetidae. Keen (1961) recognized two Recent subgenera of Dendro-poma, Dendropoma s.s. and Novastoa, as well as one extinct subgenus, Elliptovermetus (see above). Dendropoma (Dendropoma) accord-ing to Keen (1961) roughly corresponds to the group recognized here as Dendropoma s.s., typified by the Californian species D. lituella. However, one of the most conspicuous and ecologically significant species in Keen’s ver-sion of Dendropoma, “D.” maximum, has been removed to Ceraesignum n. gen., together with a newly-described Chilean species, C. robin-soncrusoei n. sp. Morton (1965) remarked that “D”. maximum was least consistent with his morphology-based concept of Dendropoma. The erection of a new genus for these two taxa was determined by their separation from other members of the “Dendropoma group” by long branches in the molecular tree, the absence of a major change in mtDNA gene order present in Dendropoma s.s. (Rawlings et al., 2001, 2010), and by such morphological characters as a divided female mantle to facilitate the at-tachment of egg capsules to the shell wall not found in Dendropoma s.s. (Table 3).
The second extant subgenus recognized by Keen (1961) was Dendropoma (Novastoa). The key differences between Dendropoma (Dendropoma) and Dendropoma (Novastoa) respectively, as defined by Keen (1961), were a tendency toward solitary and burrowing ver-sus colonial and encrusting growth, attached versus upwardly-spiraling shell forms, and a flat to concave versus convex operculum. Although Novastoa is recognized here as a distinct genus, all species besides the type that Keen (1961) included in Dendropoma (Novastoa) have now either been placed in Dendropoma proper (D. petraeum, D. tholia), likely belong there (D. corallinaceum, D. gha-naense), or cannot be placed with certainty in a current genus (Vermetus irregularis). Re-gardless, the description of five new species in this group permits a redefinition of Novastoa. The main identifying feature of this genus is the structure of the operculum, which bears

a remarkably well-developed mammilla on the internal surface of most species in the genus, including the New Zealand type spe-cies N. lamellosa. The external surface of the operculum is also composed of tightly packed, upright revolutions of the spiral lamina. This feature is not recorded from any other group of vermetids. The convex operculum that Keen (1961) attributed to N. lamellosa was found to be an error inconsistent with Morton’s (1951) detailed anatomical description.
The female mantle is undivided in all known species of Dendropoma s.s., allowing retention of the eggs within the mantle cavity even when the animal retracts further into the shell. This character is not uniquely synapomorphic (see generic Remarks), as it is Known to occur in at least two other vermetid species, but is diag-nostic for Dendropoma s.s. when compared to the closely-related taxa examined here. Keen (1961) included the Mediterranean species D. petraeum in Novastoa, but molecular evidence presented here indicates that this taxon be-longs in Dendropoma s.s. This conclusion is supported by the structure of the operculum, which is flattened and intermediate between the convex and concave opercular forms.
Hadfield et al. (1972) documented the diver- _sity of Hawaiian vermetids and adopted Keen’s _ (1961) generic classification in assigning their newly-described species. One species present-
ed in that study was Dendropoma meroclista, a minute but remarkable worm-snail with several features not previously known in Vermetidae, including a constricted, domed aperture. In light of the previously known morphological differ-ences (such as the presence of a calcified layer on the exterior surface of the operculum and a body capable of retraction deep inside the shell) and many additional characters recog-nized here (Table 3), it is therefore unsurprising that this species and several other previously unrecognized species have been placed in a new genus, Cupolaconcha. The molecular phylogeny supports the conclusion that this group is more closely related to vermetid genera such as Petaloconchus than to other members of the “Dendropoma group”. Based on species examined to date, this genus is also defined by a gene order trait: the absence of a tRNA valine gene between the ribosomal rrnS and rrnL mtDNA genes. The position of trnV, between these two ribosomal RNA genes ap-pears to be an ancestral position within the Vermetidae, and likely the Gastropoda as a whole (Rawlings et al., 2010).

88 GOLDING ET AL.

TABLE 3. Key morphological features separating Dendropoma, Novastoa, Ceraesignum n. gen. and Cupolaconcha n. gen.

Shell

Shell
Relative size
Coiling pattern

Attachment to
substratum

Feeding tube

Aperture

Sculpture on
columellar surface

Operculum
Axial profile
Calcified deposit on
exterior surface
Shape of chitinous
operculum

Mammilla

Texture on muscle
attachment area
Spiral lamina on
exterior surface

Radula
Cusps on outer
marginal tooth
Base of outer
marginal tooth

External Morphology
Length of body
relative to shell
Female mantle
margin

Reproduction
Seminal
receptacle(s)
Exhalant channel
of males
Egg capsules

Dendropoma

Small to medium
Concentric, Turritella-
squeezed-sideways,
straight or irregular
Entrenched in sub-
stratum or colonial
aggregate
Sometimes present,
short
Simple

Absent

Circular
Absent

Conical concave,
“mushroom-shaped”
or flat
Conical or nipple-
shaped
Concentric grooves

Short and flat, or
stacked

Simple

Simple

Medium

Undivided

Double

With “accessory gland” Simple

Held in mantle cavity, Attached to shell unattached

Novastoa Ceraesignum Cupolaconcha

Small to medium Medium to large Small Turritella-squeezed-
sideways

stratum or superfi-
cially attached
Present, short or
tall
Domed with a slit-
shaped aperture
Backwards-facing
teeth

Oval

Concentric Concentric,
straight or ir-
regular
Entrenched or en- Entrenched or en- Entrenched in sub-tirely embedded tirely embedded
in substratum in substratum
Sometimes Absent
present, tall
Simple Simple

Absent Absent

Circular Circular
Absent Absent

Conical concave Saucer-shaped

Conical, nipple- or Absent
spindle-shaped
Concentric “Fingerprint pat-
grooves tern”
Tall, ruffled Smooth

Simple Simple

Simple Simple

Short to medium Short to medium

Divided by long Divided by long
slit or shallow slit
notch

Single Absent

Simple

wall by stalk wall by stalk

Attached to shell

Present

Flat (plus
calcareous layers)

Absent

Dimples

Smooth

Splayed, digitiform

With a projection

Long

Divided by long slit

Single

Simple

Attached to shell
wall by stalk

“DENDROPOMA GROUP” WORM-SNAILS 89

Significance and Evolution of Morphological Characters

Recognition of species-level diversity in the “Dendropoma group’ was facilitated by enhanc-ing the dataset of morphological characters introduced by Morton (1965). While shell morphology has been used extensively to dif-ferentiate vermetid species, despite difficulties arising from extreme variability, protoconch morphology was found to be particularly useful in discriminating closely related species. Unlike previous genus-level systematic studies of vermetids, the availability of suitable material for SEM provided an excellent source of char-acters for this study. Some taxa were found to have unique microsculpture, such as the foamy crust on the protoconch of D. nebulosum and the distinctive gouges on the protoconch of D. mejillonense. The unusually complex pro-toconch morphology of C. sinaiensis n. sp. (first recognized by Safriel & Hadfield, 1988) is the primary morphological feature separat-ing this species from related taxa belonging to Cupolaconcha n. gen. Future efforts to include a wider range of vermetids may demonstrate the utility of protoconch morphology at the genus level or higher.
Unlike some vermetids, all members of the “Dendropoma group” are operculate. Morton (1965) emphasized the significance of opercu-lum morphology in separating Dendropoma s.l. from other operculate vermetids (the operculum substantially overhangs the foot and has a distinctive mammilla) and for recognizing three sub-groups within Dendropoma s.l. Morton’s (1965) subgroups do not directly correlate with any of the genera recognized here. However, results from both the morphological survey and the molecular phylogenetic analysis sup-ported the division of Dendropoma s.s. into two distinct subgroups of “concave-operculate” and “convex-operculate” taxa. The former includes the type species and most of the medium-sized species, while the latter comprises of several species that share a conserved morphology and a deeply entrenched colonial growth habit (such as Dendropoma corrodens). Although these groups have not been formally named, the concordance between the morphological and molecular datasets suggests that opercular characters are useful for analyzing relation-ships between groups of species. Operculum morphology reaches its most extreme in the “Dendropoma group” (Figs. 346-358) with Novastoa and the “convex-oper-

culate” group of Dendropoma s.s., in which the central mammilla is extended to form a spindle or rod. The functional utility of this character is unclear, although it is likely to be related to their extremely cryptic mode of life and small size relative to other vermetids. Elaboration of the mammilla, deeply anchored in the muscular foot, may improve the animals’ ability to prevent removal of the operculum during predatory events. It is interesting to note that Ceraesig-num maximum, which also lives deeply buried in coral substratum but is by an order of mag-nitude larger than members of Novastoa, has a far simpler operculum that entirely lacks a mammilla on the internal surface.
The calcified operculum of Cupolaconcha n. gen. is unique in Vermetidae. The irregular, lopsided calcified layer is fused to the external surface of a simple, flat chitinous operculum. The calcified layer is possibly created by the repeated “wiping” of the operculum inside the mantle margin, resulting in the repeated deposition of thin layers of calcified substance that when fully developed can plug the dome from the inside.
The reproductive biology of species attributed to Dendropoma s.I. has been given a mixed ac-count in the literature. Keen (1961) made no re-mark on the reproductive mode of Dendropoma s.l. Morton (1951) originally documented the divided female mantle and attached egg cap-sules of Novastoa lamellosa, but subsequently concluded that Dendropoma s.l. (including Novastoa) was united by the presence of an undivided female mantle margin, unlike other vermetids (Morton, 1965). Here we have shown that uniquely among “Dendropoma group” taxa, Dendropoma s.s. broods its unattached egg capsules in the female mantle cavity, protected by an undivided mantle. Most other known vermetids, including Ceraesignum n. gen., Novastoa and Cupolaconcha n. gen. have a female mantle that is slit to varying degrees and attach their egg capsules to the shell wall. Egg capsule size, color and egg count varied be-tween species and are useful for differentiating species. For example, the eggs of С. диапа п. sp. are mint green and contain just two or three eggs per capsule, unlike the six to 12 yellowish eggs included in each capsule of C. meroclista. Variation in capsule number is very high, as demonstrated by Calvo et al. (1998) in the D. petraeum species complex. Individuals from populations in one region of the Mediterranean can retain up to 86 egg capsules, each usually containing a single egg, while others from a

90 GOLDING ET AL.

different region brood only 12 egg capsules,
each containing 25 eggs.
Species with direct-developing larvae that
hatch as crawling juveniles, such as D. pe-
traeum, are likely to exhibit a high degree of
genetic structure among populations and more intraspecific variation in reproductive charac-teristics associated with adaptation to local environments. Others such as C. maximum with a long lived planktotrophic larva, would be expected to exhibit less genetic variation across locations. There is growing evidence to support this. In her phylogeographic study of six Pacific vermetids, Faucci (2007) demon-strated strong genetic structure even over small spatial scales in Dendropoma gregarium and D. rhyssoconchum — both species with direct development. In contrast, Thylacodes variabilis

[as Serpulorbis], a species with planktotrophic development, exhibited much less genetic variation across similar geographic scales. There seems to be a high potential for cryptic species in vermetids regardless of reproductive type, however (Faucci, 2007). While more cryp-tic taxa may be residing within those taxa with direct development (as opposed to mixed and planktotrophic development), the prevalence of cryptic taxa may also simply be reflective of the difficulty in species recognition within this family of sessile irregularly coiled worm-snails. Radular morphology in Vermetidae is gener-
ally assumed to be fairly uniform and of little re-
solving power between genera. Bandel (1984:
46) stated that because of this great intrafamil-
ial similarity “it seems unwarranted to split the
vermetids into many different genera.” Morton

FIGS. 346-358. Cross-sectional diagrams of opercula, not drawn to scale. FIG. 346: Cupolaconcha spp., calcareous layer shaded gray; FIG. 347: Ceraesignum maximum; FIG. 348: Ceraesignum rob-insoncrusoei п. sp.; FIG. 349: Novastoa lamellosa; FIG. 350: Novastoa caboverdensis п. sp.; FIG. 351: Novastoa pholetorn . sp.; FIG. 352: Novastoa batavia п. sp.; FIG. 353: Novastoa sp. (as in Table 1); FIG. 354: Dendropoma lituella and Dendropoma mejillonense; FIG. 355: Dendropoma platypus; FIG. 356: Dendropoma nebulosum; FIG. 357: Dendropoma cf. petraeum; FIG. 358: Dendropoma cf. corrodens, Dendropoma gregarium, Dendropoma howense, Dendropoma cf. tholia and Dendropoma expolitum n. sp.

“DENDROPOMA GROUP” WORM-SNAILS 91

(1965) recognized that radular morphology is generally conserved in Vermetidae, but identi-fied several minor radular characters as diag-nostic for Dendropoma. In the present study, radular characters were found to only separate the three genera Dendropoma s.s., Novastoa, and Ceraesignum from Cupolaconcha (and perhaps other groups of vermetids) because of a few minor features on the marginal teeth, but were not useful for differentiating genera or species within those groups.

Phylogenetic Relationships

Our molecular phylogeny, inferred using mtDNA and nuclear gene regions, provided an excellent opportunity to test the integrity of the morphologically defined groups. Strong support indices were recovered for each genus and for several pairs of genera and multi-genus clades (Table 2). Likewise, the presence of a gene or-der change shared among all Dendropoma s.s. provided a robust character supporting place-ment of taxa within this clade. Unfortunately, the relationships between Dendropoma s.s., Ceraesignum n. gen. and Novastoa were un-resolved, although they form a well-supported clade within Vermetidae. Nevertheless, the results reveal the striking degree of genetic divergence between these genera and rein-force the need to introduce and re-establish genus-level taxa in the group. The sampling, albeit limited, of non-“Dendropoma group” taxa was sufficient to conclude decisively that Cu-polaconcha n. gen. is not closely related to the other three genera included in this systematic revision. Overall, therefore, these molecular results provided good support for our system-atic decisions.
This is the first attempt to conduct a mo-lecular phylogenetic analysis of Vermetidae at the genus or family level, and the highly informative results suggest that an expansion of the dataset to include more of the diversity of Vermetidae will be productive. Indeed, the unusual degree of plasticity with the vermetid mtDNA genome (Rawlings et al., 2001, 2010) suggests that gene order rearrangements hold great future potential as robust phylogenetic markers defining major clades of vermetids, as already shown here for Dendropoma s.s. and Cupolaconcha. Likewise, the high levels of mtDNA sequence divergence observed within and across taxa (Rawlings et al., 2001; Faucci, 2007; Calvo et al. 2009; this study) indicates that mitochondrial gene sequences will likely

prove useful in delimiting vermetid taxa (Fau-cci, 2007; Calvo et al., 2009; Weinberger et al., 2010), exploring biogeographic patterns of diversification (Faucci, 2007), and ultimately, in inferring the evolutionary history of the family. Given that growing evidence suggests that the Vermetidae is harboring more diversity than currently realized (Faucci, 2007; Calvo et al., 2009; this study), molecular data also offer the opportunity to uncover cryptic species of vermetids. Genetic evidence, in concert with supporting morphological and ecological data, should ultimately help us to recognize the true diversity of this family.

ACKNOWLEDGMENTS

Over the many years that led to this study numerous friends and colleagues helped us with obtaining specimens above and below the water line. We especially thank Michael Hadfield (joint field work in U.S. Virgin Islands, Florida, and hosting RB in the Hawaiian Islands); Pablo Penchaszadeh, Patricia Milo-slavich and Roberto Cipriani (joint fieldwork and hosting of RB in Venezuela), Paula Mikkelsen (joint field work in Florida and Bahamas, and for providing additional material form Barbados and the Bahamas), Fred Wells (joint fieldwork and hosting of RB in Western Australia), Colin McVarish (valuable field assistance in Barba-dos) and Petra Sierwald (field help and scuba support in numerous locations).
Additional specimens were contributed to the study by Isabella Kappner (material from Jordan and Cape Verdes), Uriel Safriel (mate-rial from Sinai), John D. Taylor (material from the Maldives and Kenya), Stefano Schiaparelli (material from the Indo-Pacific), Jack Worsfold (material from the Bahamas), Aldo Pacheco (material from mainland Chile), Marta Calvo and José Templado (material from Spain), Tony Frias Martins and Ana Costa (material from the Azores), Anuschka Faucci (material from Hawaii and the Pacific Islands), Nicole Phil-lips (material from Moorea, French Polynesia), Richard and Megumi Strathmann (material from Hawaii), Louis Gosselin (material from western Canada) and Lauren Dombowsky (material from the Cayman Islands).
Formal research station visits, field work-shops, and research expeditions were sup-ported by the Bermuda Biological Station and the Bermuda Aquarium (especially Wolfgang Sterrer); Smithsonian Marine Station in Ft.

92 GOLDING ET AL.

Pierce, Florida (Mary Rice, Valerie Paul, and
staff); INTECMAR station in Puerto Cabello, Venezuela (Pablo Penchaszadeh); Pacific Biomedical Research Center (Michael Had-
field); West Indies Laboratory of the Fairleigh Dickinson University, St. Croix (John and Nancy Ogden); Bellairs Research Institute, Barbados (Judith Mendes, Director); Mote Tropical Research Laboratory, Summerland Key, Florida (David Vaughan); the Seventh International Marine Biological Workshop in the Houtman Abrolhos Islands, Western Australia (Fred Wells and Clay Bryce); Guana (Lianna Jarecki, The Falconwood Foundation); Abaco (Craig Layman and Friends of the Environ-ment); and the Smithsonian Marine Station on Carrie Bow Cay, Belize (Klaus Ruetzler, Zach-ary Foltz, Scott Jones; Caribbean Coral Reef Ecosystems Program).
Help with loans of type and other museum material and assistance during museum visits was provided by numerous individuals, includ-ing Mandy Reid (AMS); Elizabeth Kools (CAS); Regina Kawamoto (BPBM); Sergio Letelier (MNHNC); Bruce Marshall (NMNZ); Kathie Way (NHMUK); Miroslav (Jerry) Harasewych (NMNH/Smithsonian Institution); Darryl Potter (QM); Gustav Paulay and John Slapcinsky (UF); Fred Wells and Corey Whisson (WAM); Ole Tendal and Antonia Vedelsby (ZMC). Assistance with molecular procedures, in-cluding collecting, assembling and annotating nucleotide sequence data, was provided by the following summer research students at Cape Breton University: Samantha Lawrence, Martin MacInnis, Crystal MacLeod, and Kurt Simmons. As so often before, Howard Don Cameron (University of Michigan) and Rich-ard E. Petit (North Myrtle Beach) helped with linguistic and literature questions, respectively. Paul Callomon (ANSP) is thanked for help with translations from Japanese literature. Michael Hadfield and an anonymous reviewer provided valuable critique and suggestions, much but not all was followed herein.
Collecting permits were provided in the con-text of the listed workshops and expeditions. Fieldwork and specimen acquisition in Florida was partly supported by the Comer Science and Education Foundation, the Negaunee Foundation Ltd, the Grainger Foundation, and Field Museum’s Department of Zoology’s Marshall Field Fund. Specimen collecting in the protected waters of the Florida Keys was conducted under Florida Keys National Marine Sanctuary Research Permit FKNMS-2009-024 and U.S. Fish and Wildlife Service Special Use

Permit 41580-2010-20 (and earlier issues of these permits) for work in the National Wildlife Refuges. RB’s participation of the IOC 1997 expedition aboard the R/V Carlos Porter to the Chilean Juan Fernandez Archipelago and Des-venturas Islands was supported under National Geographic Foundation grant 5257 to Mark Westneat and Brian Dyer. Major funding for this project was provided under National Science Foundation awards DBI-0841760/0841777.

LITERATURE CITED

ABBOTT, К. T., 1974, American Seashells, 2nd edition. Van Nostrand Reinhold, New York, U.S.A., 663 pp.
ADAMS, H. & A. ADAMS, 1853-58, The genera of Recent Mollusca; arranged according to their organization. John van Voorst, London, 2 vols. [1: 1-256, pls. 1-32 (1853); 1: 257-484 (1854); 2: 1-92, pls. 33-72 (1854); 2: 93-284, pls. 73-96 (1855); 2: 285-412, pls. 97-112 (1856); 2: 413-540, pls. 113-128 (1857); 2: 541-660, pls. 129—138 (1858)].
ANGULO, R. J., P. C. F. GIANNINI, К. SUGUIO & L. С. В. PESSENDA, 1999, Relative sea-level changes in the last 5500 years in southern Brazil (Laguna-Imbituba region, Santa Catarina State) based on vermetid 14C ages. Marine Geology, 159: 323-339.
ANGULO, R. J., L. С. В. PESSENDA& М. С. DE SOUZA, 2002, О significado das datacöes ao 14C na reconstrucáo de paleoniveis marinhos e na evolucáo das barreiras quaternárias do litoral paraense. Revista Brasileira de Geociéncias, 32: 95-106.
ANTONIOLI, F., К. CHEMELLO, $. IMPROTA & S. RIGGIO, 1999, Dendropoma lower intertidal reef formations and their palaeoclimatological significance, NW Sicily. Marine Geology, 161: 155-170.
BANDEL, K., 1984, The radulae of Caribbean and other Mesogastropoda and Neogastropoda. Zoologische Verhandelingen, 214: 1-188, pls. 1-22.
BANDEL, K. 8 T. KOWALKE, 1997, Cretaceous Laxispira and a discussion on the monophyly of vermetids and turritellids (Caenogastropoda, Mollusca). Geologica et Palaeontologica, 31: 257-274.
BARNARD, K. H., 1963, Contributions to the knowledge of South African marine Mollusca. Part lil. Gastropoda: Prosobranchiata: Taenio-glossa. Annals of the South African Museum, 47(1): 1-199.
BIELER, R. & R. E. PETIT, 2011, Catalogue of the Recent and fossil “worm-snail” taxa of the families Vermetidae, Siliquariidae, and Turritel-lidae (Mollusca: Caenogastropoda). Zootaxa, 2948: 1-103.
BIELOKRYS, L. S., 1999, Small vermetids (Gas-tropoda) from the Mandrikovka beds. Paleon-tologicheskii Zhurnal, 5: 34—40, pl. 1.

“DENDROPOMA GROUP” WORM-SNAILS 93

BIONDI, S., 1859 ["1857”], Descrizione di alcune specie malacologiche nuove che vivono nel nos-tro littorale. Memoria 2.a. Atti dell’ Accademia Gioenia di Scienze Naturali di Catania, (Ser. 2), 12113-123831 pl Saw!
BIVONA-BERNARDI, A., 1832, Caratteri di un nuovo genere di conchiglie fossili, estratti dalle Collettanee di Storia naturale, opera manoscritta del barone Antonino Bivona Bernardi. Effemeridi Scientifiche e Letterarie per la Sicilia, 1: 55-62,
| pl. 1; 2: 3-8, pl. 2.
CALVO, M., J. TEMPLADO, M. OLIVERIO & A. MACHORDOM, 2009, Hidden Mediterranean biodiversity: molecular evidence for a cryptic species complex within the reef building ver-metid gastropod Dendropoma petraeum (Mol-lusca: Caenogastropoda). Biological Journal of the Linnean Society, 96: 898-912.
CALVO, M., J. TEMPLADO & Р.Е. PENCHASZA-DEH, 1998, Reproductive biology of the gre-garious Mediterranean vermetid gastropod Dendropoma petraeum. Journal of the Marine Biological Association of the United Kingdom, 78: 525-549.
CARPENTER, P. P. 1857, Catalogue of the col-lection of Mazatlan shells in the British Museum collected by Frederick Reigen. London, xii + 552 pp.
CHENU, J. C., 1843-1845, G[enus] Vermetus. Illustrations Conchyliologiques. [no text; pl. 1, 1843; pls. 2-5, 1844; pl. 5*, 1845].
CLESSIN, S., 1901-1912, Die Familie Vermeti-dae. Systematisches Conchylien-Cabinet von Martini und Chemnitz, 6(6), 1-124, pls. 1-15. [1-8, pls. 1-12, 1901; 36-80, pl. 13, 1902; 81-104, 1903; pls. 14-15. 1904; 105-124, 1912; pp. 9-35 are on Caecidae].
COCCO, A., 1832, Su di alcuni nuovi crustacei de’ mari di Messina. Effemeridi Scientifiche e Letterarie, 1(2): 203-209, 1 pl.
COLEMAN, F. C. & S. L. WILLIAMS, 2002, Overexploiting marine ecosystem engineers: potential consequences for biodiversity. Trends in Ecology and Evolution, 17: 40-44.
COLGAN, D. J., W. Е. PONDER, E. ВЕАСНАМ & J. MACARANAS, 2007, Molecular phyloge-netics of Caenogastropoda (Gastropoda: Mol-lusca). Molecular Phylogenetics and Evolution, 42: 717-737.
COLLINS, T. M., 1996, Molecular comparisons of transisthmian species pairs: Rates and patterns of evolution. Pp. 303-334, in: J. В. C.Jackson, А. Е. Bupo & А. С. Coates, eds., Evolution and environment in tropical America. University of Chicago Press, Chicago, ix + 425 pp. | COSSMANN, M., 1912, Loxonematacea (fin). Es-sais de Paléoconchologie Comparée. Privately printed, Paris, Livraison 9, 215 pp., 10 pls. COSSMANN, M. 8 A. PEYROT, 1922, Con-chologie Néogénique de l’Aquitaine. Tome IV Gastropodes (suite). Livraison |. Actes de la ron Linnéenne de Bordeaux, 73: 1-322, pls. 1-7.
CRISCIONE, F. & W. F. PONDER, 201A2 ph,ylo - genetic analysis of rissooidean and cingulopsoid-ean families (Gastropoda: Caenogastropoda).

Molecular Phylogenetics and Evolution, http:// dx.doi.org/10.1016/j.ympev.2012.11.026 DACCARETT, E. Y. & V. S. BOSSIO, 2011, Co-lombian seashells from the Caribbean Sea. L'Informatore Piceno, Ancona, Italy, 384 + 16 pp.
[DA COSTA, E. M.], 1770-1771, Conchology, or natural history of shells. [London]. 26 pp., 12 pls. [an unfinished anonymous publication, often attributed to Humphrey. See Jackson (1937) and Whitehead (1977).]
DALL, W. H., 1881, [Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78) and in the Caribbean Sea (1879-80) by the U.S. Coast Survey Steamer “Blake”, Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding.] XV. Preliminary report on the Mollusca. Bulletin of the Museum of Comparative Zoology, 9(2): 33-144.
DALL, W. H., 1889, [Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877-78) and in the Caribbean Sea (1879-80) by the U.S. Coast Survey Steamer “Blake”, Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bar-tlett, U.S.N., commanding.] XXIX. Report on the Mollusca. Part Il. Gastropoda and Scaphopoda. Bulletin ofthe Museum of Comparative Zoology, 18: 1-492, pls. 10-40.
D'ARGENVILLE, A.-J. D. [FAVANNE, J. DE & J. G. DE FAVANNE], 1780, La conchyliologie ou histoire naturelle des coquilles de mer, d'eau | douce, terrestres et fossile; avec une traité de
la zoomorphose, ou représentation des animaux qui les habitent: ouvrage dans lequel on trouve une nouvelle méthode de les diviser. Troisième édition. 3 vols. De Bure. vol. 1: frontispiece + i-iv + [i] + ai—aili + i-iv, plate, ix-Ix + 1878; vol. 2: frontispiece + 1-848.; vol. 3: frontispiece + pls. 1-80.
DARRIBA, D., G. L. TABOADA, КВ. DOALLO & D. POSADA, 2012, jModelTest 2: more models, new heuristics and parallel computing. Nature Methods, 9: 772.
DAUDIN, F. M., 1800, Recueil de mémoires et de notes sur des espèces inédites ou peu connues de mollusques, de vers et de zoophytes, orne de gravures. Fuchs, Treuttel & Wurtz, Paris, i-xvili, 19-50, 4 pls. [pre-5 November 1800].
DAVILA, [P. F.], 1767, Catalogue systématique et raisonné des curiosités de la nature et de l'art: qui composent le cabinet de M. Davila. Chez Briasson, Paris, Vol. 1: xxxv + [1] + 571. DILLWYN, L. W., 1817, À descriptive catalogue of Recent shells, arranged according to the Linnean method; with particular attention to the synonymy. J. & A. Arch, London, U.K., Vol. 2: 581-1092 + index.
DI TOMMASO, P., $. MORETTI, I. XENARIOS, M. OROBITG,A .M ONTANYOLA, J. -M. CHANG, J. F. TALY & C. NOTREDAME, 2011, T-Coffee: a web server for the multiple sequence alignment of protein and RNA sequences using structural information and homology extension. Nucleic Acids Research, 39 (Suppl. 2): W13-W17.

94 GOLDING ET AL.

EKAWA, K. & Y. SAKASHITA, 2013, Notes on Dendropoma dragonella (Okutani, 1975) (Gas-
tropoda: Vermetidae) from Kagoshima Prefec-
ture, Japan. Chiribotan, 42(1-4): 5-10.
FAUCCI, A., 2007, The influence of larval disper-
sal potential on speciation, phylogeography, and genetic population structure in two Pacific marine snail groups. PhD. Dissertation, Univer-sity of Hawal'i, U.S.A., 136 pp.
FINLAY, Н. J., 192A6 fur,the r commentary on New Zealand molluscan systematics. Transactions of the New Zealand Institute, 57: 320-485, pls. 18-23 [23 December].
FUKUDA, H., 1993, Marine Gastropoda (Mol-lusca) of the Ogasawara (Bonin) Islands Part 1: Archaeogastropoda and Neotaenioglossa. Tokyo Metropolitan University, Tokyo, Japan, 85 pp, 21 pls.
GARDNER, S. M., 1989, Anew vermetid from the west coast of Mexico (Gastropoda: Vermetidae). Venus, 48: 250-254.
GISCHLER, E. & R. N. GINSBURG, 1996, Cav-ity dwellers (coelobites) under coral rubble in southern Belize barrier and atoll reefs. Bulletin of Marine Science, 58: 570-589.
GOREN, М. & В. $. GALIL, 2001, Fish biodiversity in the vermetid reef of Shiqmona (Israel). Marine Ecology, 22: 369-378.
GRAY, J. E., 1842, [Mollusca], рр. 48-92. In: Syn-opsis of the contents of the British Museum, [44th Ed.]. British Museum, London, [iv] + 308 pp. GRAY, J. E., 1847, A list of the genera of Recent Mollusca, their synonyma and types. Proceed-ings of the Zoological Society of London, 15: 129-219.
GRAY, J. E., 1850, [text]. In: M. E. Gray, Figures of molluscous animals, selected from various authors. Longman, Brown, Green & Longmans, London, Vol. 4: iv + 219 pp. [August].
GRAY, J. E., 1854, List of the shells of Cuba in the collection of the British Museum, collected by M. Ramon de la Sagra, described by Prof. Alcide d’Orbigny, in the “Histoire de ГИе de Cuba.” British Museum, London, 48 pp.
HADFIELD, M. G., 1970, Observations on the anatomy and biology of two Californian vermetid gastropods. The Veliger, 12: 301-309. HADFIELD, M. G., 1989, Latitudinal effects on juvenile size and fecundity in Petaloconchus (Gastropoda). Bulletin of Marine Science, 45: 369-376.
HADFIELD, M. G., E. A. KAY, M. U. GILLETTE & M.C.LLOYD, 1972, The Vermetidae (Mollusca: Gastropoda) of the Hawaiian Islands. Marine Biology, 12: 81-98.
HARTMAN, O., 1959, Catalogue of the poly-chaetous annelids of the World. Allan Hancock Foundation Publications Occasional Paper, 23, Part |: i-vi, 1-353; Part Il: i-v, 355-628.
HEALY, J. M., 1988, Sperm morphology in Ser-pulorbis and Dendropoma and its relevance to the systematic position of the Vermetidae (Gastropoda). Journal of Molluscan Studies, 54: 295-308. |
HUGHES, R. N. & A. H. LEWIS, 1974, On the spatial distribution, feeding and reproduction of

the vermetid gastropod Dendropoma maximum. Journal of Zoology, London, 172: 531-547. HUTTON, F. W., 1873, Catalogue of the marine Mollusca of New Zealand, with diagnoses of the species. Colonial Museum and Geological Survey Department, Wellington, xx + 116 pp., all
[I.C.Z.N.] International Commission on Zoologi-cal Nomenclature, 1987, Opinion 1425. Sup-pressed: Spiroglyphus Daudin, 1800 and Stoa De Serres, 1855 (Mollusca, Gastropoda) and specific names published in combination with them. Bulletin of Zoological Nomenclature, 44(1): 57-58.
[1.C.Z.N.] International Commission on Zoological Nomenclature, 1999, International Code of Zoo-logical Nomenclature, 4th ed. 1.T.Z.N., London, xxix + 306 pp.
IREDALE, T., 1937, Middleton and Elizabeth Reefs, South Pacific Ocean. Australian Zoolo-gist, 8: 232-261, pls. 15-17.
IRVING, R.A., 1995, Near-shore bathymetry and reef biotopes of Henderson Island, Pitcairn Group. Biological Journal of the Linnean Soci-ety, 56: 309-324.
JACKSON, J. W., 1937, A letter from George Humphrey to William Swainson, 1815. Journal of Conchology, 20(12): 332-337.
JONG, К. M. bE & H. E. COOMANS, 1988, Marine gastropods from Curagao, Aruba and Bonaire. Studies on the Fauna of Curacao and other Caribbean Islands, 69: 1-261, pls. 1-47. КАРРМЕК, I., 1998, Spatial distribution, popu-lation structure and feeding behaviour of the worm-snail Dendropoma maxima (Gastropoda, Vermetidae) in the Gulf of Aqaba. Center for Tropical Marine Ecology (ZMT), Bremen, Ger-many, M.Sc. Dissertation, University of Bremen, Germany.
KAPPNER, |., $. M. AL-MOGHRABI & С. RICHTER, 2000, Mucus-net feeding by the vermetid gastropod Dendropoma maxima in coral reefs. Marine Ecology Progress Series, 204: 309-313.
KAY, Е. A., 1979, Hawaiian marine shells; reef and shore fauna of Hawaii Section 4: Mollusca. Bernice P. Bishop Museum Special Publication, 64(4): xvili + 653 pp.
KEEN, A. M., 1961, A proposed reclassification of the gastropod family Vermetidae. Bulletin of the British Museum (Natural History), Zoology, 7(3): 183-213, pls. 54-55. |
КЕЕМ, А. M., 1971a, Two new supraspecific taxa inthe Gastropoda. The Veliger, 13(3): 296. KEEN, A. M., 1971b, Sea shells of tropical west America — Marine mollusks from Baja Califor-та to Peru, 2nd ed. Stanford University Press, Stanford, California, xiv + 1064 pp.
KEEN, A. M., 1980, Siphonium, an over-used name in Mollusca. The Festivus, 12(10): 125-126.
KEEN, A. M., 1983, Vermetidae of the tropical eastern Pacific. The Western Society of Mala-cologists Annual Report, 15(1982): 10.
КЕЕМ, А. М. & М.С. HADFIELD, 1985, Spirogly-phus Daudin, 1800 and Stoa De Serres, 1855

“DENDROPOMA GROUP” WORM-SNAILS 99

(Mollusca, Gastropoda, Vermetidae): proposed suppression of two equivocal generic names. Z.N.(S.) 2340. Bulletin of Zoological Nomen-clature, 42(1): 46-49.
KEEN, А. M. & J. E. MORTON, 1960, Some new African species of Dendropoma (Vermetidae: Mesogastropoda). Proceedings of the Mala-cological Society of London, 34(1): 36-51, pls. 2-4.
KELLY, W. C., Ill, 2007, Three new vermetid gastropod species from Guam. Micronesica, 39: 117-140.
KURODA, T., 1928, Catalogue ofthe shell-bearing Mollusca of Amami-Oshima (Oshima, Osumi). Kagoshima-ken Kyoiku Chosa-kai [Kagoshima Prefectural Educational Investigation Commit-tee], vii + 126 pp.
LABOREL, J., Е. LABOREL-DEGUEN, $. PAPA-GEORGIOU, J. EVAN, Р.А. PIRAZZOLI & C. S. STIROS, 2000, Seismic coastal uplift in a region of subsidence: Holocene raised shorelines of Samos Island, Aegean Sea, Greece. Marine Geology, 170: 41-58.
LEA, H. C., 1843, Description of some new fossil shells from the Tertiary of Virginia. Proceedings ofthe American Philosophical Society, (new ser. 3): 162-165.
LINK, H. F., 1807, Beschreibung der Naturalien-Sammlung der Universität zu Rostock. Mol-lusken. Adlers Erben, Rostock, 2-3: 82-160; 4: 6-23.
MAES, V. O., 1967, The littoral marine molluscs of Cocos-Keeling Islands (Indian Ocean). Pro-ceedings of the Academy of Natural Sciences of Philadelphia, 119: 93-217.
MAURY, C. J., 1922, Recent Mollusca of the Gulf of Mexico and Pleistocene and Pliocene species from the Gulf States; Part 2: Scaphopoda, Gas-tropoda, Amphineura, Cephalopoda. Bulletins of American Paleontology, 9(38): 33-173. MIKKELSEN, P. M., К. BIELER, I. KAPPNER &T . A. RAWLINGS, 2006, Phylogeny of Veneroidea (Mollusca: Bivalvia) based on morphology and molecules. Zoological Journal of the Linnean Society, 148: 439-521.
MILOSLAVICH, P. A. & P. E. PENCHASZADEH, 1992, Reproductive biology of Vermetus sp. and Dendropoma corrodens (Orbigny, 1842): two vermetid gastropods from the southern Caribbean. The Veliger, 35: 78-88. MONTEROSATO, T., 1884a, Nomenclatura gener-ica e specifica di alcune conchiglie mediterranee. Palermo, Stab. Tipografico Virzi, 152 pp. MONTEROSATO, T., 1884b, Conchiglie littorali mediterranee. Fam. Vermetidae. Naturalista Si-ciliano, Palermo, 4: 60-63 [a copy of the ver-metid text in 1884a].
MORCH [as MOERCH], O. A. L., 1859, Etudes sur la famille des vermets. Journal de Conchy-liologie, 7: 342-360 (June).
MORCH [as MOERCH], O. A. L., 1860, Études sur la famille des vermets (suite). Journal de Conchyliologie, 8: 27-48 (January).
MORCH, О.А. L., 1861, Review of the Vermetidae (Part). Proceedings ofthe Zoological Society of London, 1861: 145-181, pl. 25 (September).

MORCH, O.A.L., 1862, Review ofthe Vermetidae (Part Il.). Proceedings of the Zoological Society of London, 1861: 326-365 (April).
MÖRCH, О. A. L., 1877, Synopsis molluscorum marinorum Indiarum occidentaliumi m primis In-sularum danicarum. Malakozoologische Blätter, 24: 93-123.
MORHANGE, C. & P.A. PIRAZZOLI, 2005, Mid-Holocene emergence of southern Tunisian coasts. Marine Geology, 220: 205-213. MORRISON, J. P. E., 1968, Spiroglyphics: a study in species association. The American Malacological Union Inc, Annual Reports, for 1968: 45-46.
MORTON, J. E., 1951, The structure and adapta-tions of the New Zealand Vermetidae. Part Ill. Novastoa lamellosa and its affinities. Transac-tions and Proceedings of the Royal Society of New Zealand, 79: 43-51, pls. 8, 9.
MORTON, J. E., 1955, The evolution of vermetid gastropods. Pacific Science, 9(1): 3-15. MORTON, J. E., 1965, Form and function in the evolution of the Vermetidae. Bulletin of the Brit-ish Museum (Natural History) (Zoology), 11(9): 585-630.
OKUTANI, T., ed., 2000, Marine Mollusks in Ja-pan. Tokai University Press, Tokyo, xlviii +1,174 pp. [with contributions by multiple authors; Ver-metidae (рр. 205-209) by К. Hasegawal]. OKUTANI, T. & T. HABE, 1975, [The mollusks of Japan. (Sea snails) — |]. Gakken Illustrated Nature Encyclopedia, Mollusca (I). Gakken, Tokyo, 301 pp.
ORBIGNY, A. D’, 1841-1853, Mollusques. In: R.Sacra, Histoire physique, politique, et na-turelle de ГИе de Cuba. 2 vols. and atlas [is-sued as of 1853, but published in parts earlier, as follows: French edition, 1: 1-264 (1841); 2: 1-112, pts. 1-7 (1842); 113-380, pts. 8-24 (by 1853; exact dates to be clarified). The Spanish ed., with title page dated 1845, translated from and published after the French ed.] PACHECO,A. & J. LAUDIEN, 2008, Dendropoma mejillonensis sp. nov., a new species of vermetid (Caenogastropoda) from northern Chile. The Veliger, 50(3): 219-224.
PALUMBI, S.R., 1996, Nucleic acids Il: the poly-merase chain reaction. Pp. 205-221, in: D. M. Hittis, С. Moritz & B. K. MabLe, eds., Molecular systematics, 2nd ed. Sunderland, Massachu-setts: Sinauer Associates, xvi + 655 PP.
PARK, J.K. & D. Ô FOIGHIL, 2000, Sphaeriid and corbiculid clams represent separate heterodont bivalve radiations into freshwater environments. Molecular Phylogenetics and Evolution, 14: 75-88.
PEYROT-CLAUSADE, M. P. HUTCHINGS & С. RICHARD, 1992, Temporal variations of mac-roborers in massive Porites lobata on Moorea, French Polynesia. Coral Reefs, 11: 161-166. PHILLIPS, N. E., 2011, Where are larvae of the vermetid gastropod Dendropoma maximum on the continuum of larval nutritional strategies? Marine Biology, 158: 2335-2342.
PHILLIPS, М.Е. & 4.5. SHIMA, 2010, Reproduc-tion of the vermetid gastropod Dendropoma

96 GOLDING ET AL.

maximum (Sowerby, 1825) in Moorea, French
Polynesia. Journal of Molluscan Studies, 76:
133-137.
PONDER, W. F., 1967, Anew species of Dendro-
poma from New Zealand (Mollusca: Vermeti-
dae). Transactions ofthe Royal Society of New Zealand, 10(2): 17-20, pl. 1.
POWELL, А. W. В., 1979, New Zealand Mollusca — Marine, Land and Freshwater Shells. Williams Collins Publishers Ltd., Auckland, New Zealand, xv + 500 pp.
QUOY, [J. В. C.] 4 [J. P.] GAIMARD, 1834-1835, Voyage de découvertes de l’Astrolabe exécuté par ordre du Roi, pendant les années 1826- 1827-1828-1829, sur le commandement de M. J. Dumont d’Urville. Zoologie, Mollusques. J. Tastu, Paris, Vol. 3: 1-366 (1834), 367-954 (1835), atlas 107 pls.
КАМВАЧТ, А. & А. J. DRUMMOND, 2007, Tracer v1.4, available from http://beast.bio.ed.ac.uk/ Tracer
RAWLINGS, T. A., Т. M. COLLINS & К. BIELER, 2001, A major mitochondrial gene rearrange-ment among closely related species. Molecular Biology and Evolution, 18: 1604-1609. RAWLINGS, T. A., M. J. MACINNIS, R. BIELER, J. L. BOORE & T. M. COLLINS, 2010, Sessile snails, dynamic genomes: gene rearrangements within the mitochondrial genome of a family of caenogastropod mollusks. BMC Genomics, 11:
440. doi:10.1186/1471-2164-11-440
REHDER, H. A., 1981, The Audubon Society field guide to North American seashells. Alfred A. Knopf, New York, 894 pp.
RILOV, G., Y. BENAYAHU & A. GASITH, 2004, Prolonged lag in population outbreak of an inva-sive mussel: a shifting-habitat model. Biological Invasions, 6: 347-364.
RONQUIST, Е. & J. P HUELSENBECK, 2003, Mr-Bayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics, 19: 1572-1574. ROSENBERG, G., 2009, Malacolog 4.1.1: A Database of Western Atlantic Marine Mollusca. [WWW database (version 4.1.1)], ULR http:// www.malacolog.org/
ROSENBERG, С., Е. MORETZSOHN & Е. Е. GARCIA, 2009, Gastropoda (Mollusca) of the Gulf of Mexico. Pp. 579-699, in: D. L. FELDER € О. К. Camp, eds., Gulf of Mexico — origins, wa-ters, and biota: biodiversity. Texas À & M Press, College Station, Texas, 1,393 pp.
SAFRIEL, U., 1966, Recent vermetid formation on the Mediterranean shore of Israel. Proceed-ings of the Malacological Society of London, 37: 27-34.
SAFRIEL, U. & M. G. HADFIELD, 1988, Sibling speciation by life-history divergence in Den-dropoma (Gastropoda; Vermetidae). Biological Journal of the Linnean Society, 35: 1-13. SCAPS, P. & V. DENIS, 2008, Can organisms associated with live scleractinian corals be used as indicators of coral reef status? Atoll Research Bulletin, 566: 1-18.
SCHATTNER, P., А. N. BROOKS & Т. M. LOWE, 2005, The tRNAscan-SE, snoscan and snoGPS web servers for the detection of tRNAs and

snoRNAs. Nucleic Acids Research, 2005: W686-W689.
SCHIAPARELLI, S., С. ALBERTELLI 8 К. CAT-TANEO-VIETTI, 2006, Phenotypic plasticity of Vermetidae suspension feeding: a potential bias in their use as biological sea-level indicators. Marine Ecology, 27: 44-53.
SCUDERI, D., 1995, Il genere Dendropoma (Gastropoda, Vermetidae) nel Mediterraneo. Bollettino Malacologico, 31(1-4): 1-6. SERRES, M. be, 1855, Note sur un nouveau genre d'Annélide tubicole perforant. Annales des Sciences Naturelles, (Ser. 4), Zoologie, 3: 238-243, pl. 8.
SHIMA, J. S., C. W. OSENBERG & A. C. STIER, 2010, The vermetid gastropod Dendropoma maximum reduces coral growth and survival. Biology Letters, 6: 815-818.
SHIMA, J. S., N. E. PHILLIPS 8 C. W. OSEN-BERG, 2013, Consistent deleterious effects of vermetid gastropods on coral performance. Journal of Experimental Marine Biology and Ecology, 439: 1-6.
SILENZI, S., Е. ANTONIOLI & В. CHEMELLO, 2004, A new marker for sea surface tempera-ture trend during the last centuries in temper-ate areas: vermetid reef. Global and Planetary Change, 40: 105-114.
SISMA-VENTURA, G., В. GUSNER, К. YAM, M. FINE & A. SHEMESH, 2009, The reef builder gastropod Dendropoma petreaum [sic] — a proxy of short and long term climatic events in the eastern Mediterranean. Geochimica et Cosmochemica Acta, 73: 4376-4383. SMALLEY, T. L., 1984, Possible effects of intraspecific competition on the population structure of a solitary vermetid mollusc. Marine Ecology Progress Series, 14: 139-144. SOWERBY, С. B., I, 1825, A catalogue of the shells contained in the collection of the late Earl of Tankerville, arranged according to the Lamarckian conchological system; together with an Appendix, containing descriptions of many new species. London, vii + 92 + xxxiv [Appendix] pp., 9 pls.
SOWERBY, С. B., II, 1839, A conchological manual. London, U.K., v + 130 pp., 24 pls. [pre 23 February].
STIER, A. C., С. $. МсКЕОМ & С. W. OSEN-BERG, 2010, Guard crabs alleviate deleterious effects of vermetid snails on a branching coral. Coral Reefs, 29: 1019-1022. | SUTER, H., 1913, Manual of the New Zealand Mollusca. John Mackay, Wellington, xxiii + 1,120 pp.
SWOFFORD, D. L., 2002, PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Meth-ods). Version 4. Sinauer Associates, Sunder-land, Massachussetts, U.S.A.
TAYLOR, J. B., 1975, Planktonic prosobranch veligers of Kaneohe Bay. Unpublished PhD dissertation, University of Hawaii, xiii + 593 pp.
THOMAS, L. H. 8 4. STEVENS, 1991, Communi-ties of constructional lips and cup reef rims in Bermuda. Coral Reefs, 9: 225-230.

“DENDROPOMA GROUP” WORM-SNAILS QT

TOMLIN, J. R. Le B., 1939, A new South African vermetid. Journal of Conchology, 21(4-5): 145, pl. 12;
TUNNEL, J. W., JR., J. ANDREWS, N. С. BAR-RERA & F. MORETZSOHN, 2010, Encyclope-dia of Texas seashells; identification, ecology, distribution, and history. Texas A& M University Press, College Station, Texas, xi + 512 pp. TRYON, G. W., 1886, Family Vermetidae. Manual of Conchology, 8: 163-191, 224-257 (index and synonymy), 436-446 (plate captions), pls. 30, 49-58.
VELAIN, C., 1876, Sur le faune malacologique des iles Saint-Paul et Amsterdam. Comptes Rendus des Séances de l’Académie des Sci-enc83e: s284,-28 7.
VELAIN, C., 1877, Expedition Francaise aux îles Saint-Paul et Amsterdam. Observations générales sur la faune des deux îles suivies d'une description des mollusques. Archives de Zoologie Expérimentale et Générale, 6: 1-143, pls. 1-5.
VESCOGNI, A., F. R. BOSELLINI, M. REUTER & Т. С. BRACHERT, 2008, Vermetid reefs and their use as palaeobathymetric markers: new insights from the Late Miocene of the Mediter-ranean (southern Italy, Crete). Palaeogeogra-phy, Palaeoclimatology, Palaeoecology, 267: 89-101.
VOKES, H. E. 8 E. H. VOKES, 1983, Distribution of shallow-water marine Mollusca, Yucatan Pen-insula, Mexico. Mesoamerican Ecology Institute Monograph 1. Middle American Research Insti-tiute Publication, 54: 1-183, incl. 50 pls.

WEINBERGER, V. P., P. MILOSLAVICH 4 A. MACHORDOM, 2010, Distributional pattern, reproductive traits, and molecular analysis of two coexisting vermetid gastropods of the ge-nus Petaloconchus: a Caribbean endemic and
a potential invasive species. Marine Biology, 157: 1625-1639.
| WHITEHEAD, P. J. P., 1977, Emanuel Mendes da Costa (1717-91) and the Conchology, or natural history of shells. Bulletin of the British Museum (Natural History), Historical Series, 6(1), 1-24. WOOD, W., 1828, Index Testaceologicus; or a catalogue of shells, British and foreign, arranged to the Linnean system; with the Latin and Eng-lish names, references to authors, and places where found, 2nd edition. Wood, London, xxii + 11] #212 pp, 38.pls,
YONGE, C.M., 1932, Notes on feeding and diges-tion in Pterocera and Vermetus, with a discus-sion on the occurrence о the crystalline style in the Gastropoda. Great Barrier Reef Expedition 1928-29. Scientific Reports, 1: 259-281. ZHANG, D. Y., 2011, Antiguan shallow-water seashells — a collection with 18 years study and research of shoreline shells from Antigua and West Indies. MDM Publishing, Wellington, Florida, xi + 211 pp.
ZVULONI, А., К. ARMOZA-ZVULONI & У. LOYA, 2008, Structural deformation of branching corals associated with the vermetid gastropod Dendro-poma maxima. Marine Ecology Progress Series, 363: 103-108.

Revised ms. accepted September 28, 2013 .